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THE HARVESTMEN FAMILY PHALANGODIDAE. 1. THE NEW GENUS *CALICINA*, WITH NOTES ON *SITALCINA* (OPILIONES: LANIATORES)

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ABSTRACT: The Californian phalangodid genus *Sitalcina* Banks is shown to be polyphyletic, and is restricted to include only those species closely related to the type species *Sitalces californica* Banks. A new genus, *Calicina,* described to accommodate most of the remaining species, is defined by the presence of a tarsal spur on the male palpus, penis glans with apically directed stylus, ovipositor with double row of apical setae, and ovipositor cuticle with microspines. At least the first of these characters is a synapomorphy.

Of the 25 species of *Calicina* recognized, 18 are transferred from *Sitalcina*: *breva* Briggs (elevated from subspecies), *cloughensis* Briggs and Hom, *digita* Briggs and Hom, *ensata* Briggs, *kaweahensis* Briggs and Hom, *keenea* Briggs, *macula* Briggs, *mariposa* Briggs, *minor* Briggs and Hom, *morroensis* Briggs, *palapraeputia* Briggs, *piedra* Briggs, *polina* Briggs, *sequoia* Briggs and Hom, *serpentinea* Briggs and Hom, *sierra* Briggs and Hom, *topanga* Briggs, and *yosemitensis* Briggs. The remaining species are new: *arida, basalta, conifera, diminua, dimorphica, galena,* and *mesaensis.*

Based on genitalic characters, primarily glans structure, four species groups and nine subgroups are recognized. Their relationships are hypothesized using cladistic analysis and vicariance biogeography. The distribution of *Calicina* is strongly concordant with that of the slender salamander, *Batrachoseps,* and with the presumed distributions of exotic terranes.

Interspecific variation in the somatic morphology of *Calicina* appears to be the result of paedomorphosis and troglobism. These modifications, present in most species, are probably adaptations to xeric environments and, possibly, competition with other phalangodids.

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Introduction

A major problem in the systematics of harvestmen is the apparent scarcity of reliable generic characters. This stems largely from the classic studies of Roewer (e.g., 1923) which overemphasized the importance of easily visible somatic characters, such as variation in the tarsal count, in defining genera. This practice has resulted in a confusing proliferation of small and monotypic genera. For example, the 17 known species of the eastern Nearctic Phalangodidae are currently assigned to eight genera (Goodnight and Goodnight 1942, 1967).

In sharp contrast to this general trend is the treatment of the phalangodids of California: only two genera are recognized for an unusually rich fauna of 39 described species. One of these, *Banksula* Roewer, includes strictly cavernicolous species having uniformly high tarsal counts (4-6-5-6) and the other, *Sitalcina* Banks, contains epigean species with lower counts (3-5-5-5 or less). Recent studies (Briggs 1974; Briggs and Ubick 1981) have demonstrated that *Banksula* is well defined by both somatic and genitalic characters: the palpal femur is armed with dorsal spines and the penis has a bifurcate ventral plate. On the other hand, Briggs (1968) found no derived character uniting the 29 species of *Sitalcina*. He even commented on the heterogeneity of the genus, listing interspecific differences in size, tarsal count, presence or absence of eyes, and type of sexually dimorphic structures. He tentatively arranged the species into three groups: (1) those with sexually dimorphic trochanters, (2) those with sexually dimorphic palps, and (3) those lacking sexual dimorphisms. However, in the absence of additional characters and because of the overall somatic similarity of the species, he did not question the validity of the genus.

Our present investigations of the genitalic morphology of *Sitalcina* indicate that the genus is indeed polyphyletic. The strongest evidence comes from the morphology of the penis where, on the basis of the glans structure, two groups of species are evident. The first is characterized by a folded, caudally directed glans that swings open 180° along a dorsoapical arc during expansion (Fig. 1b). The second is characterized by an apically directed glans that expands by a rectilinear, telescoping movement out of the shaft (Fig. 6f, g). Such striking genitalic differences are comparable to those used to distinguish families (Martens 1986).

It is now evident that *Sitalcina* must be restricted to include only those species closely related to the type species, *Sitalces californica* Banks. This monophyletic group, corresponding to group "1" of Briggs (1968), is defined by the characters listed in Table 1. In addition to the folding glans, all *Sitalcina* males have trochanteral spurs on leg IV (Fig. 1a). The ovipositor of *Sitalcina* is distinctive in various features, of which the imbricate cuticle sculpturing is possibly synapomorphic.

The nine species that now comprise *Sitalcina* (along with three others still unplaced that apparently belong to other genera) will be treated in a future paper. The purpose of this study is to describe the new genus represented by the remaining species, for which we propose the name *Calicina*. The species of *Calicina* are revised and their morphological and spatial relationships hypothesized using cladistics and vicariance biogeography. Analyses of natural history and ecology are provided.

Materials and Methods

The 800 specimens examined during the course of this study were collected almost exclusively by Briggs and associates over the past two decades. Specimens from early collections were originally stored in Oudemans' Fluid, which gave excellent initial preservation (Briggs 1968:3). However, it is now evident that prolonged storage in this solution (about 10 years or more) discolors the specimens, results in deterioration of the internal tissues, and makes genitalic extraction difficult. By comparison, specimens preserved in 75% to 85% ethanol for much longer periods do not show signs of such damage.

The genitalia can usually be extracted by simply opening the operculum and squeezing the abdomen with forceps. When this fails it is necessary to push out the genitalia carefully with a probe inserted into the anal region or, as a last resort, to dissect it out of the body cavity. Males often require additional treatment with KOH in order to fully expand the glans, which normally lies retracted within the shaft. For this, entire specimens are soaked in cold 10% KOH solution for about two minutes and then transferred to a water bath where, aided by gentle squeezing of the abdomen, maximum expansion can occur.

TABLE 1. COMPARATIVE MORPHOLOGY OF *SITALCINA* AND *CALICINA*.

	Sitalcina	*Calicina*
Total length	1.50–2.40 mm	0.77–1.67 mm
Eyes	present	present or absent
Tarsal count	3-5-5-5	3-5-5-5 to 3-3-4-4
Palp		
Patella	3 spine-bearing tubercles	2 spine-bearing tubercles
Tarsus (♂)	unmodified	with spur (usually)
Leg IV		
Trochanter (♂)	with spur	unmodified
Penis		
Glans	folding	telescoping
Ovipositor[1]		
Shape	bent	straight
Cuticle	imbricate[2]	with microspines
Apical setae		
Shape	apically hooked[3]	evenly bent
Length	long—cross at center	shorter
Number	12–20	12, rarely 14 or 16
Arrangement	not grouped[4]	in triads
Subapical setae		
Number	none	1–3 pairs, rarely none

[1] Species of *Sitalcina* examined: *californica, borregoensis, madera, scopula,* and *sura.*
[2] In *S. californica.*
[3] Except *S. scopula.*
[4] Except *S. sura.*

Unless otherwise indicated, the specimens examined during this study, including all primary types, are deposited at the California Academy of Sciences. Additional specimens are from the collections of the American Museum of Natural History (AMNH) and the University of California at Berkeley (UCB).

Complete species descriptions are given for new species; additional descriptions for those treated by Briggs (1968). All specimen measurements are in millimeters.

ABBREVATIONS FOR COLLECTORS

AGG—Andy G. Grubbs
AK—Albert Kurz
AKSJ—Albert K. S. Jung
AL—Albert Lee
BL—Benton Leong
BM—Barbara Martin
CF—C. Fox
DB—D. Broussard
DCR—D. Craig Rudolph
DR—David Rentz
DU—Darrell Ubick
EVI—E. VanIngen
GAM—G. A. Marsh
GL—Galen Leung
GT—Gordon Tang
JG—Joseph Gee
JRH—J. R. Helfer
JSB—J. S. Buckett
KH—Kevin Hom
KK—K. Kay
LMS—L. M. Smith
MG—Michael Gardner
MM—M. McEachern
MW—Michael Wong
NB—N. Boice
RL—Robert Lem
ROS—Robert O. Schuster
SK—S. Kubota
SO—Stefan Ong
SW—Steve Winterath
TO—Toshiro Ohsumi
TSB—Thomas S. Briggs
VFL—Vincent F. Lee
WCR—Warren C. Rauscher
WES—Warren E. Savary
WI—Wilton Ivie

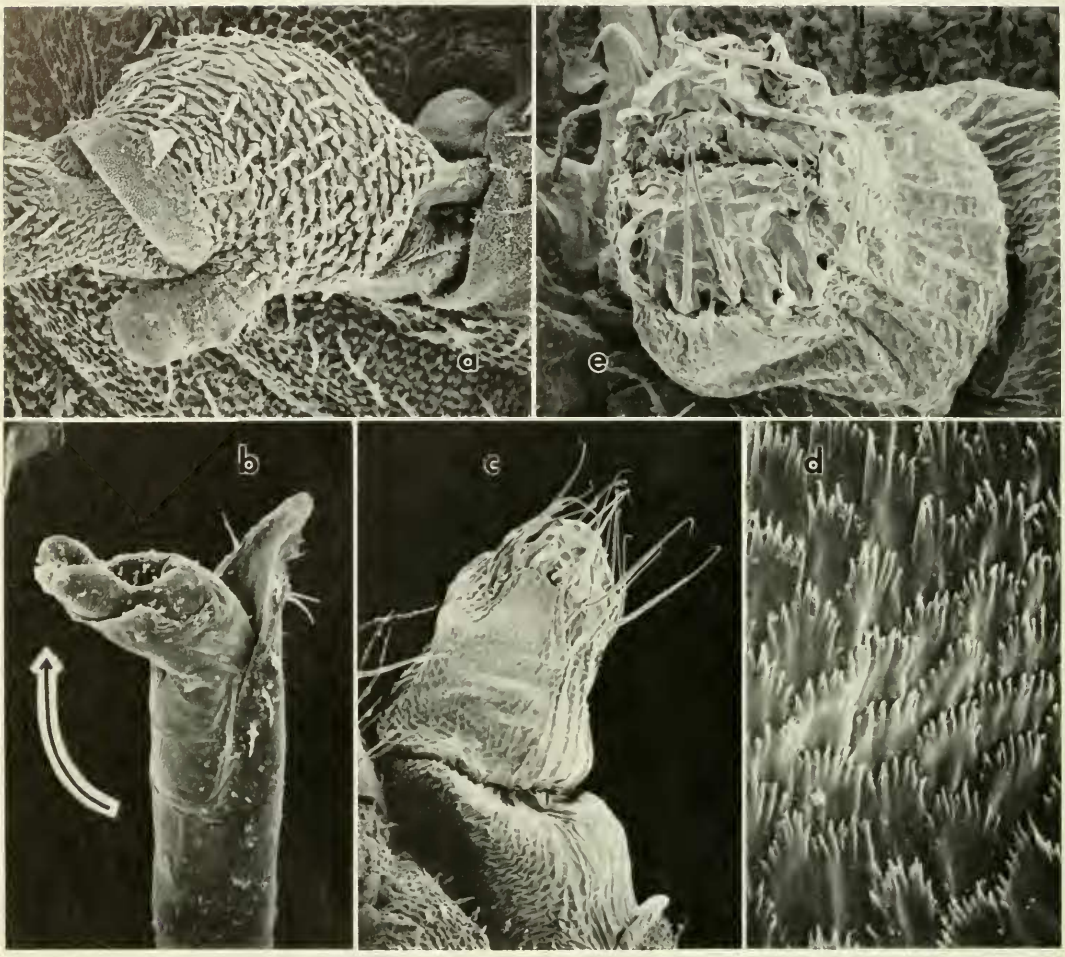


FIGURE 1. *Sitalcina californica*. (a) Trochanter IV of male, lateral view (180×). (b) Expanded glans penis, sublateral view (240×). Arrow indicates movement of glans during expansion. (c) Ovipositor, lateral view (180×). (d) Ovipositor, close-up of lateral surface showing imbricate cuticle (1,800×). (e) Ovipositor, apical view (300×).

TAXONOMY

Family PHALANGODIDAE Simon
Subfamily PHALANGODINAE Simon

Calicina Ubick and Briggs, new genus

DIAGNOSIS.—Males of *Calicina* are unique among the Nearctic phalangodid genera in having a telescoping penis glans (as opposed to a folding one). Additionally, most males of *Calicina* have a dorsal spur on the palpal tarsus, which is not known in other phalangodids. Females are distinct from those of *Sitalcina*, and possibly other genera, in having ovipositors with a double setal fringe and a cuticle with microspines. Most species of *Calicina* may be distinguished from other phalangodid genera by their reduced tarsal counts of less than 3-5-5-5.

TYPE SPECIES.—*Sitalcina mariposa* Briggs, 1968.

ETYMOLOGY.—The generic name is a contraction of California *Sitalcina* and is feminine in gender.

DESCRIPTION.—Body length 0.77–1.67. Color ranges from pale yellow to orange to reddish-brown. Body cuticle minutely and densely tuberculate, with scales, setae, and nipplelike tubercles. Scute with prominent ocular tubercle at anterior margin; varying in size, shape, and degree of rugosity (see Briggs 1968, fig. 45–57, 59, 62, 63, 65, 66). Eyes well developed (Fig. 3a) or reduced, lacking retina and occasionally cornea

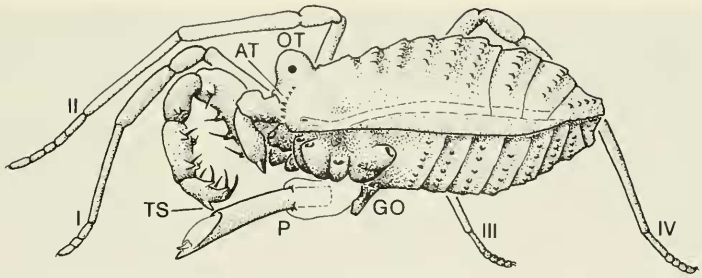


FIGURE 2. *Calicina mariposa*, lateral view of male (left appendages omitted). AT = anterior tubercles, OT = ocular tubercle, TS = tarsal spur of palpus, GO = genital operculum, P = penis, legs numbered.

(=lens) (Fig. 3b). Carapace with two rows of anterior tubercles numbering from 0 to 4 or rarely to 8 pairs (Fig. 2, 3a, b). Ozopore well developed, on anteriolateral margin, with distinct posterior channel. Tergites I–V fused, VI–VIII free, with median, transverse row of tubercles interspersed with short setae. Venter textured similarly as scute but more densely setose; seven free sternites with median, transverse rows of tubercles. Genital operculum between coxae IV, apically truncate in males, rounded in females. Coxae I and II with endites.

Leg sculpturing consisting of minutely tuberculate scales; calcanei and tarsi smooth. Leg II longest, leg length formula (longest to shortest) II,IV,I,III. Tarsal counts 3-5-5-5, 3-4-4-5, or 3-4-4-4; rarely 3-5-4-5 or 3-3-4-4. Tarsal claws single on legs I and II; paired on legs III and IV. Juveniles with hind claws on onychium, arolium between paired claws. Palpi and chelicerae distally setose, with smooth cuticle of appressed scales. Palpi robust, ventrally armed with spine-bearing tubercles (femur with three ectobasally and one mesodistally; patella with 1 pair; tibia and tarsus with 2 pairs each) (Fig. 3c). Male palpal tarsus with a well developed dorsal spur (Fig. 4a), with vestigial spur (Fig. 4b), or without spur; occasionally with enlarged mesal spine-bearing tubercle (Fig. 4c, d).

Penis without muscles, composed of basal sac, shaft, and apical glans. Basal sac inflatable. Shaft (=truncus) cylindrical, sclerotized; length 3.5–7 × width; apicoventral part (=ventral plate) rounded or attenuated, set with setae. Glans telescoping, with basal segment and stylus, rarely with additional (middle) segment (*palapraeputia*). Collar lobes (=?*Titillator* of Martens 1986) on basal segment (*mariposa* and *digita* groups), on middle segment (*palapraeputia*), or apparently absent (*serpentinea* group). Stylus apical and variable in shape. Accessory structures either thin, scalelike parastyli (=?*Konduktor* of Martens 1986) (*digita* group) or robust, lobed dorsal process (*serpentinea* group).

Ovipositor short, straight, and cylindrical when expanded; length 1.5–2.0 × width; divided into basal and distal segments. Lateral and/or apical surface covered with minute, pointed tubercles (microspines). Apex with 2 or 4 lobes, occasionally with dorsal folds; with setal fringe of 12 apical setae (10 in *diminua*) grouped in triads and 1–4 pairs of subapical setae (most species) or with 14 apical setae only (*palapraeputia* and *serpentinea* subgroup); occasionally with a pair of apical teeth (Fig. 5).

DISTRIBUTION AND SPECIES.—The genus *Calicina* is found only in the central Sierra Nevada and the Coast Ranges of California. The 25 known species represent four species groups and nine subgroups.

Key to the *Calicina* Species Groups and Subgroups Based on Characters of the Male Genitalia

1. Basal glans segment with a pair of collar lobes (Fig. 16a–d) 2
– Basal glans segment without collar lobes (Fig. 16e–h) 7
2. Parastyli absent (Fig. 6, 10a–d) 3
– Parastyli present (Fig. 7–9, 10e–h) (*digita* group) 4
3. Collar lobes simple (Fig. 6) ..... *mariposa* group and subgroup
– Collar lobes bilobed (Fig. 10a–d) ..... *arida* subgroup, in part (*cloughensis*)
4. Parastyli ventral (Fig. 7) ..... *digita* subgroup
– Parastyli lateral or dorsal 5
5. Parastyli lateral, broad and ornate (Fig. 8) ..... *kaweahensis* subgroup

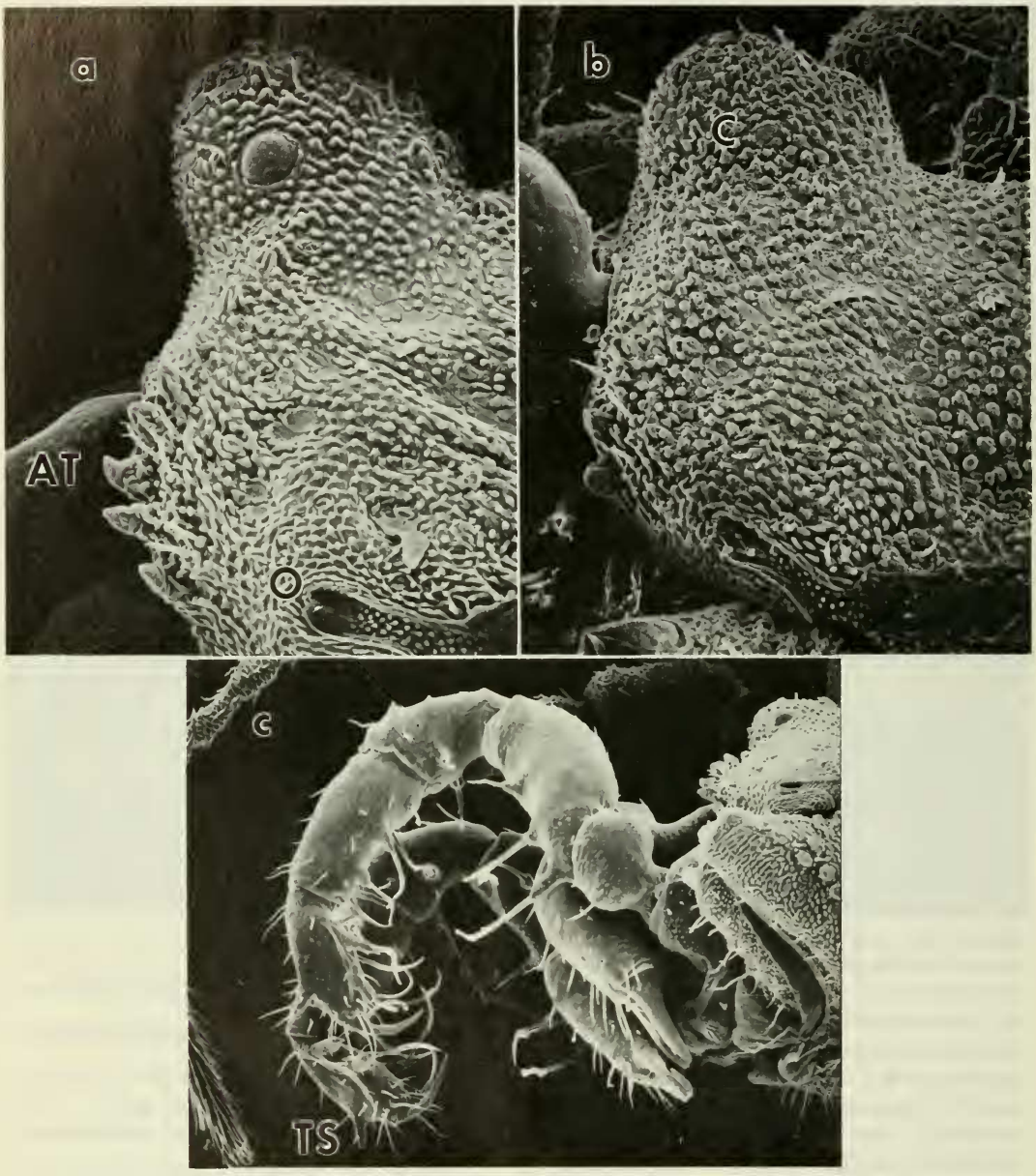


FIGURE 3. *Calicina*, morphology. (a) *C. mariposa*, male paratopotype, anterior part of scute showing ocular tubercle with large cornea, a row of paracular anterior tubercles (AT), and the ozopore (O) (230×). (b) *C. serpentinea*, female, same view showing reduced number of anterior tubercles and degenerate cornea (C) (230×). (c) *C. mariposa*, male paratopotype, chelicerae and palpi showing tarsal spurs (TS) (80×).

– Parastyli dorsal, narrow 6
6. Parastyli separate; stylus straight; ventral plate acuminate (Fig. 9) ... *topanga* subgroup
– Parastyli fused; stylus sinuous; ventral plate unmodified (Fig. 10e–h) ..... *arida* subgroup, in part (*arida*)
7. Middle segment of glans completely surrounding stylus; collar lobes hornlike (Fig. 11) ..... *palapraeputia* group and subgroup
– Middle segment of glans forming the dorsal process that is distinct from stylus; lobes variable (Fig. 16g, h) ... (*serpentinea* group) 8

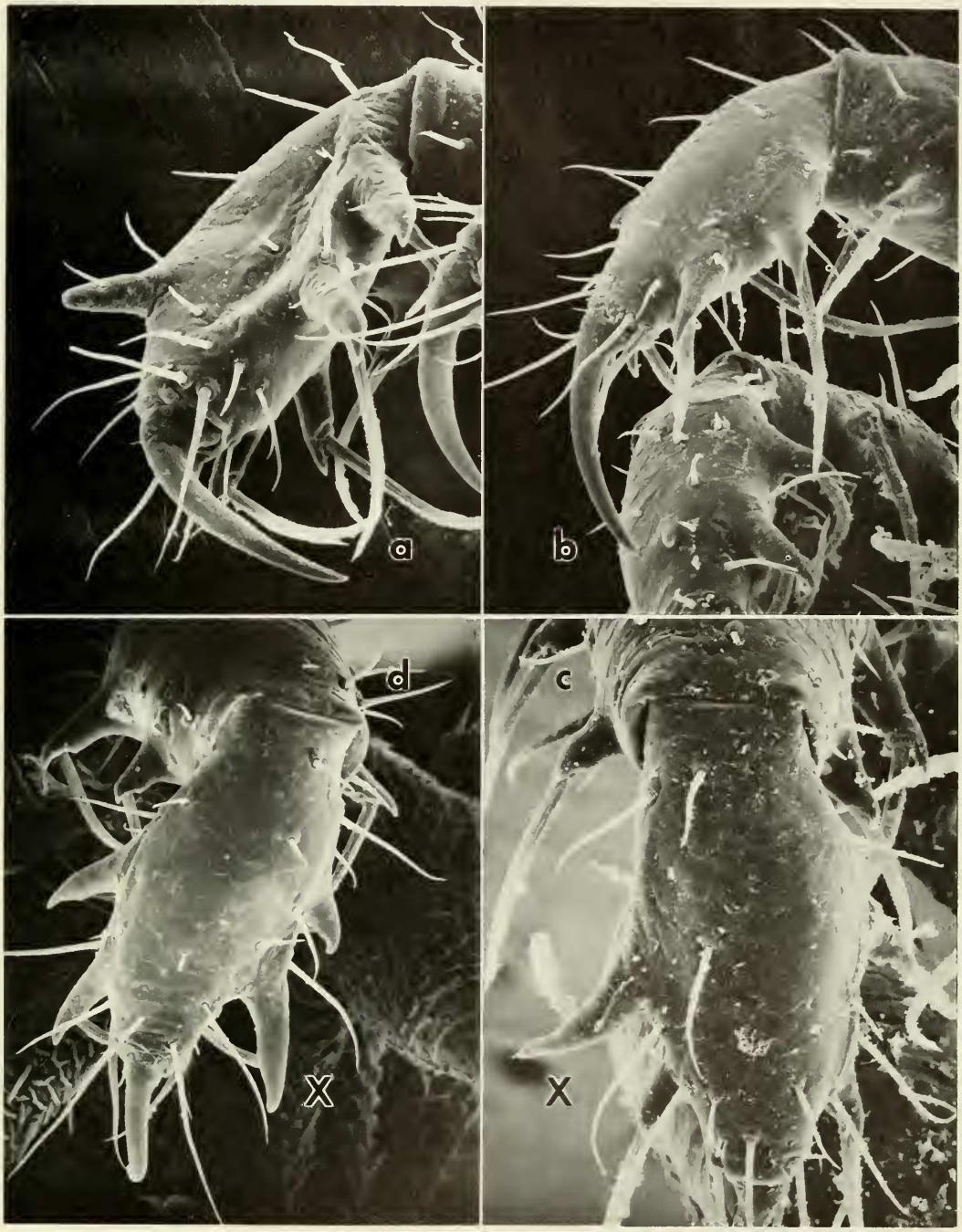


FIGURE 4. *Calicina*, male palpal tarsi. (a) *C. mariposa*, showing large tarsal spur (310×). (b) *C. mesaensis*, showing reduced tarsal spur (310×). (c) *C. minor*, showing enlarged mesobasal spine-bearing tubercle (X) (470×). (d) *C. ensata*, showing enlarged mesoapical spine-bearing tubercle (X) (310×).

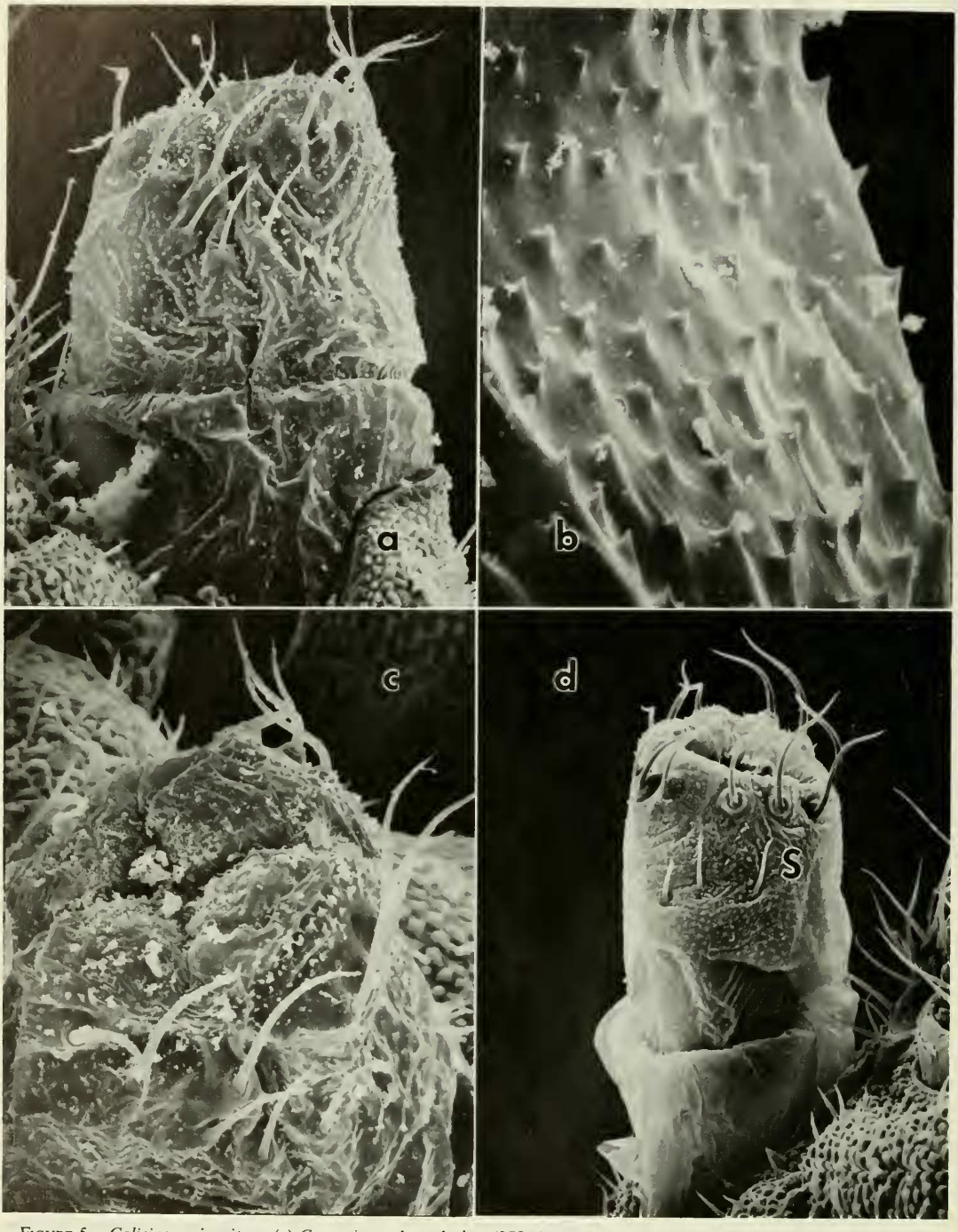
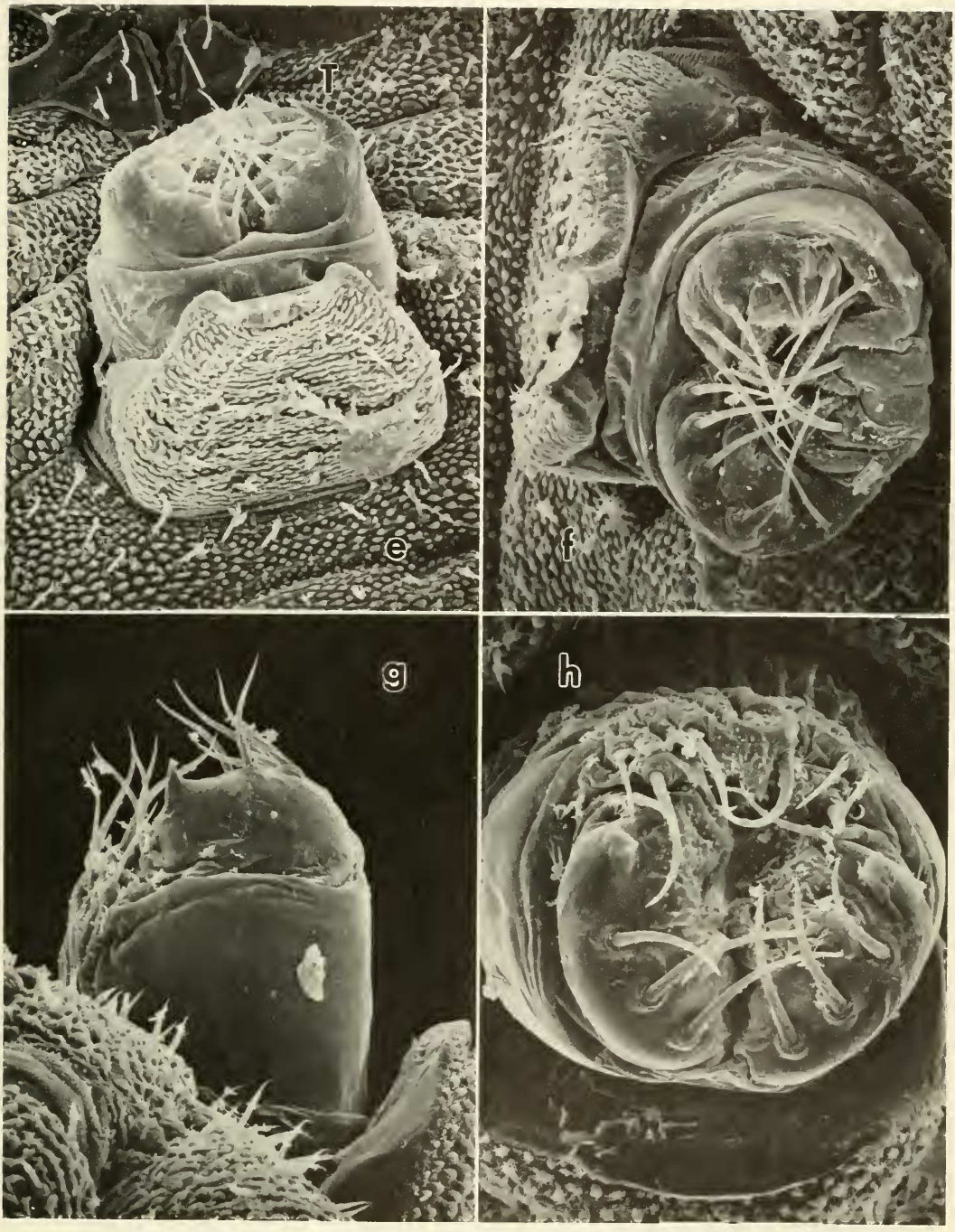


FIGURE 5. *Calicina*, ovipositors. (a) *C. mariposa*, lateral view (270×). (b) *C. mariposa*, close-up of lateral surface showing microspines (2,700×). (c) *C. mariposa*, apical view (390×). (d) *C. topanga*, lateral view showing subapical setae (S) (230×). (e) *C. palapraeputia*, ventral view showing apical tooth (T) (170×). (f) *C. palapraeputia*, apical view showing microspines and anterior margin of genital operculum (230×). (g) *C. serpentinea*, lateral view showing apical tooth (310×). (h) *C. serpentinea*, apical view showing microspines (390×).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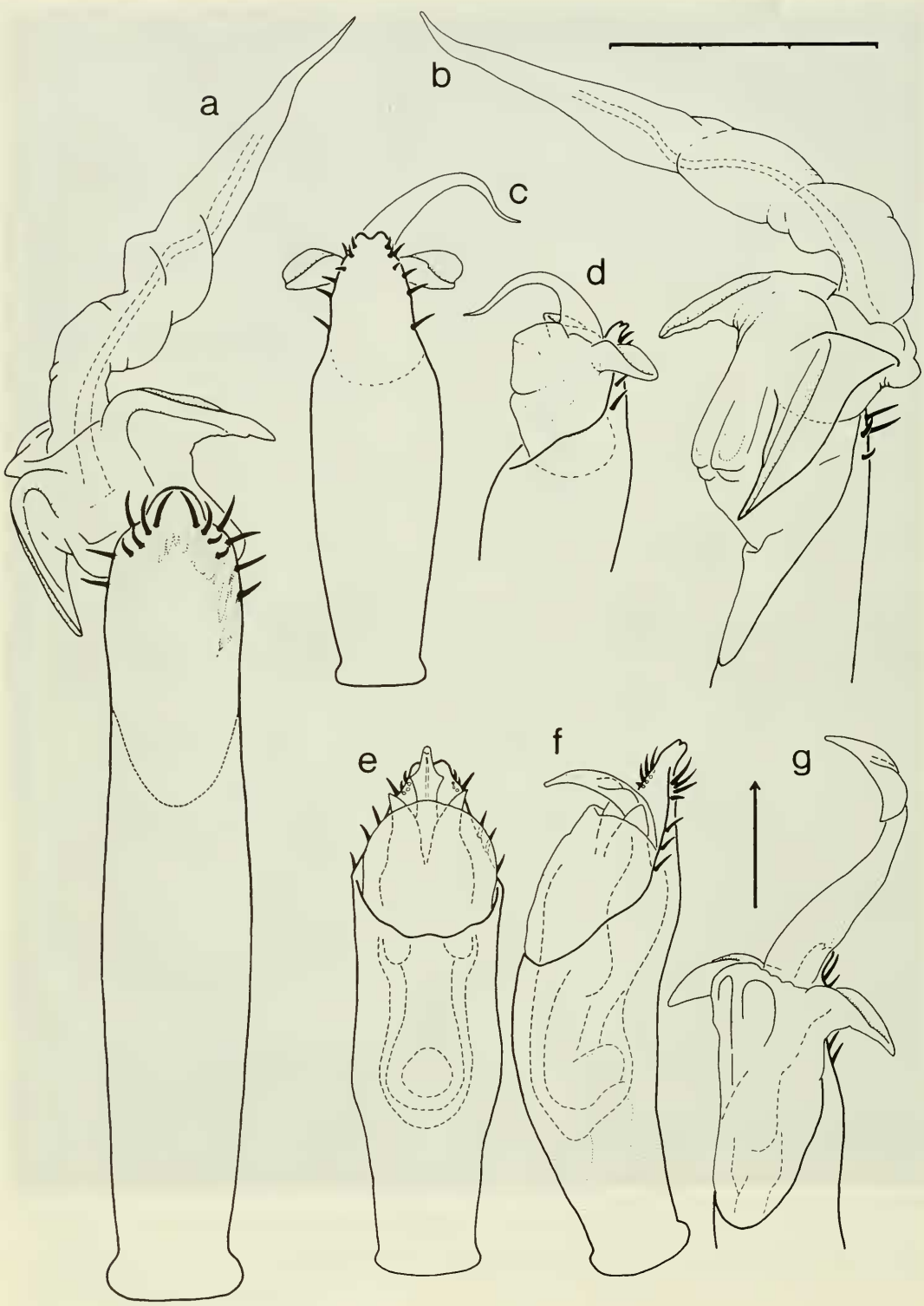
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8. Dorsal process with apical bifurcation (Fig. 12) ..... *minor* subgroup
- Dorsal process with apical lobes 9
9. Dorsal process with 5 apical lobes; ventral plate with at most 4 pairs of lateral setae (Fig. 13, 14) ..... *serpentinea* subgroup
- Dorsal process with at most 4 apical lobes; ventral plate with 5 to 8 pairs of lateral setae (Fig. 15) ..... *sequoia* subgroup

The *mariposa* Species Group (The *mariposa* Subgroup)

Diagnosis.—Members of the *mariposa* group may be recognized by their simple genitalia. The glans consists of a stylus and a basal segment bearing collar lobes and lacks additional sclerites. The ovipositor contains the full complement of 12 apical and 3 pairs of subapical setae. The dorsal grooves on the collar lobes are synapomorphic for the group. The three species belonging to this group are all summer-active forest dwellers.

Distribution.—The *mariposa* group is found only in the central Sierra Nevada in Yosemite National Park at elevations of 1,200–2,000 m.

Calicina mariposa (Briggs, 1968), new combination

(Fig. 2, 3a, c, 4a, 5a–c, 6a, b, 16a, b)

Sitalcina mariposa Briggs, 1968:31.

Diagnosis.—This species differs from other members of the group in having a high tarsal count of 3-5-5-5; males lack an apical notch on the ventral plate of the penis.

Additional Description.—Carapace with 6–8 pairs of anterior tubercles. Penis large; ventral plate apically entire and with 8 pairs of marginal setae; collar lobes pointed and pocketlike; stylus long and sinuous. Ovipositor with 12 apical setae and 3 pairs of lateral, subapical setae; microspines on apical and lateral surfaces.

Type Specimens.—Male holotype, female allotype, and three paratypes (one male, two females), under logs in a giant sequoia grove at Mariposa Big Trees, Yosemite National Park, Mariposa County, 28 July 1967, TSB and KH.

Specimens Examined.—Four males, 12 females.

New Records.—MARIPOSA COUNTY: Mariposa Big Trees, 26 July 1984 (TSB, SK, GT); TUOLUMNE COUNTY: Yosemite National Park: Tioga Pass Road, June 1970 (TSB); 9.2 km E Crane Flat Junction, 27 July 1984 (TSB, SK, GT); Wawona Camp, 17 Sep. 1941 (WI; AMNH collection).

Natural History.—Known from sequoia and yellow pine forests; collected from June to September.

Calicina yosemitensis (Briggs, 1968), new combination

(Fig. 6e–g)

Sitalcina yosemitensis Briggs, 1968:31.

Diagnosis.—Males of this species have a glans with a uniquely modified stylus tip; females may be separated from other group members in having an ovipositor with only 1 pair of subapical setae.

Additional Description.—Carapace with 4–8 pairs of anterior tubercles. Penis medium-sized; ventral plate with apical notch and 7 pairs of lateral setae; collar lobes small, pointed, apically grooved; stylus tip with lateral expansions. Ovipositor as in *mariposa* but with only 1 pair of subapical setae.

Type Specimens.—Male holotype, female allotype, and three paratypes (two males, one female), under fallen bark in coniferous forest 5.0 mi (8.0 km) E Crane Flat Ranger Station, Yosemite National Park, Tuolumne County, 28 July 1967, TSB and AL.

Specimens Examined.—Five males, three females.

New Record.—TUOLUMNE COUNTY: Yosemite National Park: 3.8 mi (6.1 km) NE Crane Flat Ranger Station, 21 July 1968 (TSB, MW, GL).

Calicina conifera Ubick and Briggs, new species

(Fig. 6c, d)

Diagnosis.—This species differs from others in the *mariposa* group by its small size, pale coloration, and absence of retina.

Etymology.—The specific name refers to the coniferous biome in which this species lives.

Description.—Color yellowish orange. Car-

←

Figure 6. Male genitalia of the *mariposa* group. (a, b) *C. mariposa* (Crane Flat Junction), ventral and lateral views. (c, d) *C. conifera* (holotype), ventral and lateral views. (e–g) *C. yosemitensis*. (e, f) Dorsal and lateral views showing retracted glans (paratopotype). (g) Dorsolateral view showing expanded glans, arrow indicates movement of glans during expansion (3.8 mi NE Crane Flat). Note: Unless otherwise indicated, the scale bar for these and all subsequent genitalic drawings equals 0.30 mm, and all drawings are of fully expanded glandes.

apace with 3 or 4 pairs of anterior tubercles. Retina absent, lens present. Tarsal count 3-4-4-5.

Male: Total body length, 1.20. Scute length, 0.80. Scute width, 0.88. Eye tubercle length, 0.12. Eye tubercle width, 0.16. Leg II length, 2.13. Palpal tarsus with dorsal spur. Penis small; ventral plate apically notched and with 7 pairs of marginal setae; collar lobes small, rounded and apically grooved; stylus uniformly tapering and sinuous.

Female: Total body length, 1.00. Scute length, 0.63. Scute width, 0.71. Eye tubercle length, 0.13. Eye tubercle width, 0.11. Ovipositor as in *mariposa* but with two pairs of subapical setae.

Type Specimens.—Male holotype and two female paratypes, under fallen bark in a mixed coniferous forest at 1.8 km E Crane Flat Junction, Tuolumne County, 29 July 1984, TSB, SK, and GT.

Specimens Examined.—Only the type series.

The *digita* Species Group

Diagnosis.—The parastyli on the glans penis is the presumed synapomorphy for this group.

The *digita* Subgroup

Diagnosis.—The *digita* subgroup is distinguished from all others by the unique male genitalia: the ventral plate is arrow-shaped and the glans bears a pair of slender, ventral parastyli. Males have a large dorsal spur on the palpal tarsus.

Distribution.—Middle elevation Sierra Nevada from Amador south to Tulare counties.

Calicina digita (Briggs and Hom, 1967), new combination

(Fig. 7a–d, 16c, d)

Sitalcina digitus Briggs and Hom, 1967:51. Briggs, 1968:20.

Diagnosis.—This species is easily distinguished from the other in its subgroup by a higher tarsal count of 3-5-5-5.

Additional Description.—Carapace with 6 or 7 pairs of anterior tubercles. Glans with a pair of short, scalelike parastyli and long, sinuous stylus. Ventral plate with 7 pairs of setae. Ovipositor similar to that of *mariposa* but with lower density of microspines and with 2 or 3 pairs of subapical setae.

Type Specimens.—Male holotype, female allotype, and 20 paratypes (12 males, eight females), under fallen bark at 2.2 mi (3.5 km) S Giant Forest, Sequoia National Park, Tulare County, 15 May 1966, TSB and KH.

Specimens Examined.—Twenty-seven males, 22 females.

New Records.—MARIPOSA COUNTY: 3 mi (5 km) E Briceburg, 6 Feb. 1954 (ROS; AMNH collection); Merced River, N Fork near Main Fork, 31 Mar. 1983 (TSB, SO). FRESNO COUNTY: Saturday Cave, near Boyden Cave, 15 May 1966 (TSB); Big Creek, 7 Aug. 1956 (ROS; UCB collection). TULARE COUNTY: Sequoia National Park: 0.9 mi (1.4 km) S Giant Forest Village, 17 Aug. 1984 (TSB, VFL, DU); 4 mi (6.4 km) N Hospital Campground, 13 Feb. 1967 (JSB, MG).

Natural History.—Found in a variety of biomes, including forests (giant sequoia-yellow pine forest, oak woodland) and grassland, and collected throughout the year. There is one collection from a cave.

Remarks.—The disjunct populations do not appear to differ in reproductive or somatic characters.

Calicina sierra (Briggs and Hom, 1967), new combination

(Fig. 7e–g)

Sitalcina sierra Briggs and Hom, 1967:49.
Sitalcina sierra sierra Briggs and Hom. Briggs, 1968:20.

Diagnosis.—*Calicina sierra,* a paedomorphic species, is most readily distinguished from *digita* by its low tarsal count of 3-4-4-4.

Additional Description.—Carapace with 3 or 4 pairs of anterior tubercles. Penis similar to, but smaller than, that of *digita.* Ovipositor as in *mariposa.*

Juveniles.—One of the two juveniles is an early instar (from Scat Cave) having a tarsal count of 1-1-2-2, the other is a penultimate (McLean's Cave area, 2 Nov. 1975) just prior to moulting. Both instars lack anterior tubercles. The late instar has several robust spines on each of the free tergites; the early instar has only one pair of such spines restricted to tergite VII. The eyes of both instars are well developed, as in adults.

Type Specimens.—Male holotype, female allotype, and five paratypes (three males, two females), 6.2 mi (10.0 km) N Mercer Caverns, Sheep Ranch Road, Calaveras County, 26 Mar. 1966, TSB and KH.

Specimens Examined.—Forty-three males, 30 females, two juveniles.

New Records.—CALAVERAS COUNTY: Music Hall Cave, 7.2 km ESE Angel's Camp, 18 May 1977 (AGG, SW, MM, NB); Carlow's Bat Cavern, 7 km SE Angel's Camp, 25 May 1977 (DB, SW, AGG); Scat Cave, 4 mi (6.4 km) W Columbia, 26 Mar. 1979 (BM, SW); unnamed cave, Peruvian Gulch, 2 mi (3.2 km) NW Columbia, 10 May 1980 (DU); Speleogen Cave, 7 km SE Angel's Camp, 20 Apr. 1980 (TSB, DU). TUOLUMNE COUNTY: Lower van Trump Mine, Fox Gulch,

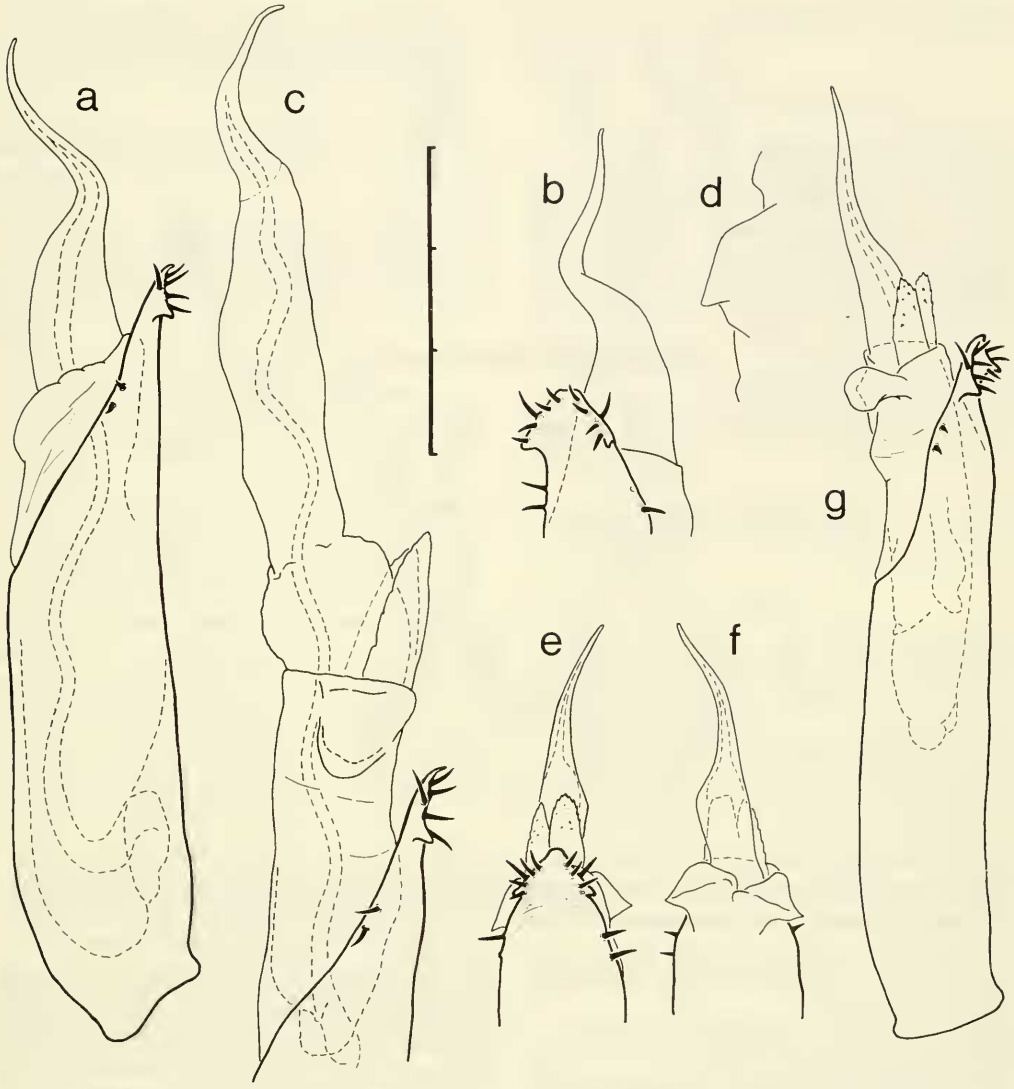


FIGURE 7. Male genitalia of the *digita* subgroup. (a–d) *C. digita*. (a, b) Lateral and subventral views showing retracted glans (Merced River). (c, d) Lateral view of expanded glans and dorsal view of left collar lobe (Giant Forest). (e–g) *C. sierra* (McLean's Cave area), ventral, dorsal, and lateral views.

23 Sep. 1975 (TSB, RL); Porcupine Skull Cave, 2 mi (3.2 km) N Columbia, 11 Feb. 1979 (DCR, SW); 2.5 mi (4 km) NW Columbia, 2 Feb. 1979 (DCR, SW); S Fork Stanislaus River at Marble Quarry Road, 5 Mar. 1981 (DU); 2.5 mi (4 km) N Columbia, McLean's Cave area, 2 Nov. 1975 (TSB, RL), 2 Apr. 1979 (DCR, BM, SW).

DISTRIBUTION.—Known from Amador, Calaveras, and Tuolumne counties.

NATURAL HISTORY.—Found in digger pine-oak forests during the winter and spring months (November–April). *C. sierra* is also known from caves, where it is active throughout the year, although it has never been collected in association with the sympatric, cavernicolous species of *Banksula*. In an extensive survey of the Calaveras Formation caves, *Banksula* was recorded from more than 30 caves and *C. sierra* from six different ones (Briggs and Ubick 1981).

The *kaweahensis* Subgroup

DIAGNOSIS.—Males of the *kaweahensis* subgroup are unique in having a penis with ornate, lateral parastyli.

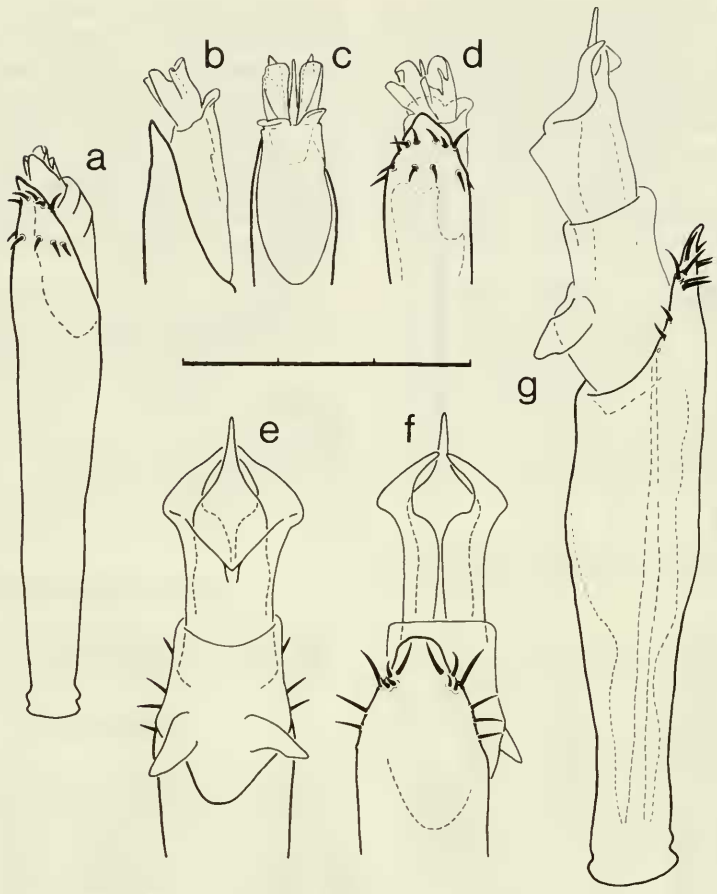


FIGURE 8. Male genitalia of the *kaweahensis* subgroup. (a–d) *C. galena.* (a) Sublateral view showing retracted glans (holotype). (b–d) Lateral, dorsal, and ventral views (paratopotype). (e–g) *C. kaweahensis* (Rocky Hill), dorsal, ventral, and lateral views.

DISTRIBUTION.—Known only from Tulare County.

Calicina kaweahensis (Briggs and Hom, 1966), new combination

(Fig. 8e–g)

Sitalcina kaweahensis Briggs and Hom, 1966:266. Briggs, 1968: 22.

DIAGNOSIS.—This species may be distinguished by the combination of large size (body length greater than 1.4 mm) and a tarsal count of 3-5-4-5. Males have a glans with uniquely modified parastyli.

ADDITIONAL DESCRIPTION.—Carapace with 4 pairs of anterior tubercles. Penis with collar lobes in basal position; parastyli dorsally fused and apically attenuated; stylus straight and basally enlarged; ventral plate with 8 pairs of marginal setae. Ovipositor as in *mariposa* but with 2 pairs of subapical setae and with a pair of large apical teeth; microspines on entire distal segment but sparse on the ventral surface.

TYPE SPECIMENS.—Female holotype, male allotype, and two paratypes (damaged), under granitic rocks at 0.3 mi (0.5 km) N Junction of Woodlake-Lemoncove Road on road to Badger, Tulare County, 26 Nov. 1965, TSB and VFL.

SPECIMENS EXAMINED.—Seventeen males, 11 females, four specimens of undetermined sex (damaged).

NEW RECORDS.—TULARE COUNTY: 0.3 mi (0.5 km) N junction Woodlake-Lemoncove Road, 18 Dec. 1965 (KH); near Lake Kaweah Offices on Hwy 198, 14 May 1966 (TSB); near Kaweah Dam on Hwy 198, 26 Nov. 1965 (VFL); 2.1 mi (3.4 km) E Rocky Hill Town, 19 Dec. 1966 (TSB, KH); 1.4 mi (2.3 km) E Rocky Hill, 22 Jan. 1967 (TSB, KH, AKSJ); Yokohl Valley, near Lindsay, Feb. 1971 (TSB); Three Rivers, Nov. 1967 (TSB).

NATURAL HISTORY.—Known from oak woodland biomes and collected throughout the winter and spring months (November–May).

Calicina galena Ubick and Briggs, new species
(Fig. 8a–d)

DIAGNOSIS.—Males of this species differ from all others by the ornately scrolled parastyli and the unique transverse rows of setae on the ventral plate.

ETYMOLOGY.—The specific name refers to the type locality and is a name in apposition.

DESCRIPTION.—Carapace with 1 pair of anterior tubercles. Eyes present. Tarsal count 3-5-5-5 or 3-5-4-5.

Male: Total body length, 1.17. Scute length, 0.79. Scute width, 0.72. Eye tubercle length, 0.17. Eye tubercle width, 0.12. Leg II length, 1.94. Color yellowish orange. Palpal tarsus without dorsal spur. Penis with ventral plate bearing 6 pairs of setae arranged in two transverse rows; collar lobes reduced to small flaps; parastyli intricately scrolled; stylus short and spinelike.

Female: Total body length: 1.01. Scute length, 0.69. Scute width, 0.78. Eye tubercle length, 0.13. Eye tubercle width, 0.12. Color orange. Ovipositor as in *mariposa*.

VARIATION.—Some specimens from the Johnsondale localities have the basal tarsomeres of tarsus III fused, giving a tarsal count of 3-5-4-5.

JUVENILES.—The single known juvenile is very pale, has a tarsal count of 3-5-4-5, and has well developed eyes. As in adults, one pair of anterior tubercles is present, and the abdominal tergites lack robust setae.

TYPE SPECIMENS.—Male holotype and 11 paratypes (two males, eight females, one juvenile), Galena Creek, Mountain Home State Forest, Tulare County, 4 Sep. 1967, TSB. Ten paratypes (seven males, three females), 2.25 mi (3.6 km) W Johnsondale, Tulare County, 1,600 m, 2 July 1988, TSB and DU. Nineteen paratypes (12 males, seven females), Double Bunk Meadows, 3.5 air mi (5.6 km) SW Johnsondale, Tulare County, 1,850 m, 3 July 1988, TSB and DU.

SPECIMENS EXAMINED.—Only the type series.

NATURAL HISTORY.—The original series was collected beneath granite rocks in a giant sequoia forest. The recent collections are from mixed coniferous forests; specimens were collected beneath and within decaying logs, large slabs of fallen bark, and dense mats of duff. The population at 3.6 km W Johnsondale is sympatric with a species of *Sitalcina*.

The *topanga* Subgroup

DIAGNOSIS.—This subgroup is distinguished from all others by several unique male genital characters: apex of ventral plate attenuated and armed with two pairs of strong setae; stylus straight and elongated, somewhat flattened; parastyli short, hornlike in shape and dorsally situated; and collar lobes small and covered with minute tubercles.

DISTRIBUTION.—Members of this subgroup occur in the southern Coast Ranges and Tehachapi Mountains, the southernmost distribution of the genus.

Calicina topanga (Briggs, 1968), new combination
(Fig. 5d, 9c, d)

Sitalcina topanga Briggs, 1968:25.

DIAGNOSIS.—This species may be distinguished from others in the subgroup by its high tarsal count of 3-5-5-5.

ADDITIONAL DESCRIPTION.—Carapace with 2 or 3 pairs of anterior tubercles. Penis with ventral plate attenuated and bearing 7 pairs of setae, of which four apical ones are enlarged; collar lobes earlike lateral projections with microspines; parastyli dorsal, short and hornlike; stylus long and straight, somewhat flattened. Ovipositor as in *mariposa* but with 2–4 pairs of subapical setae (one specimen with 9 setae).

TYPE SPECIMENS.—Male holotype, female allotype, and four paratypes (two males, two females), under sandstone in a dense oak forest at 3.3 mi (5.3 km) N Topanga Beach in Topanga Canyon, Los Angeles County, 7 Apr. 1966, TSB, KH, and VFL.

SPECIMENS EXAMINED.—Thirty-eight males, 32 females, one specimen of undetermined sex.

NEW RECORDS.—SANTA BARBARA COUNTY: Santa Ynez Mountains, Cold Springs, 19 Dec. 1967 (TSB, AKSJ). Santa Cruz Island: canyon N UCSB Field Station, 19 Dec. 1967 (TSB, KH, AKSJ), 21 Dec. 1967 (TSB); 0.1 mi (0.2 km) SW UCSB Field Station, 20 Dec. 1967 (AKSJ); Cañada del Puerto, Prisoners Harbor, 21 Dec. 1967 (KH, AKSJ); Raven's Wood Canyon, 22 Dec. 1967 (TSB); Cristi Pines, 19–22 Dec. 1967 (TSB, KH, AKSJ).

NATURAL HISTORY.—Known from both closed and open forests (broadleaf evergreen, digger pine-oak, and oak woodland), and collected during the winter and spring months (December–April).

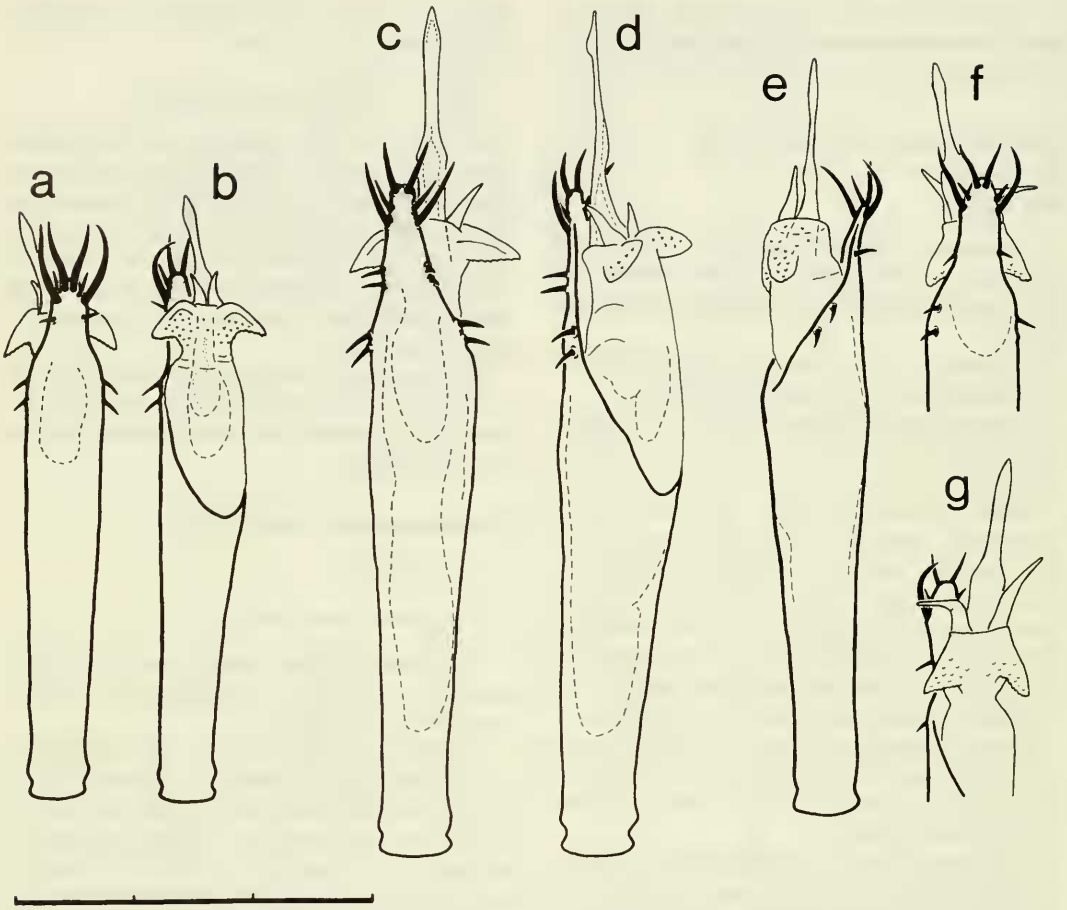


FIGURE 9. Male genitalia of the *topanga* subgroup. (a, b) *C. morroensis* (Madonna Inn), ventral and subdorsal views. (c, d) *C. topanga* (Santa Cruz Island), subventral and lateral views. (e–g) *C. keenea* (holotype), lateral, ventral, and dorsal views.

REMARKS: The mainland and island populations of *topanga* appear similar in both genitalic and somatic characters.

Calicina keenea (Briggs, 1968), new combination

(Fig. 9e, f)

Sitalcina keenea Briggs, 1968:25.

DIAGNOSIS.—This species is distinguished from others in its group by its tarsal count, 3-4-4-5.

ADDITIONAL DESCRIPTION.—Carapace with 2 or 3 pairs of anterior tubercles. Penis similar to but smaller than that of *topanga*; ventral plate with 6 pairs of lateral setae. Ovipositor as in *mariposa* but with 4 pairs of subapical setae and with a lower density of microspines.

TYPE SPECIMENS.—Male holotype and female allotype, under granite in moist oak grassland at 3.2 mi (5.1 km) NW Keene, Kern County, 19 Mar. 1967, VFL.

SPECIMENS EXAMINED.—Only the type series.

Calicina morroensis (Briggs, 1968), new combination

(Fig. 9a, b)

Sitalcina morroensis Briggs, 1968:26.

DIAGNOSIS.—This paedomorphic species differs from others in the group by the combination of low tarsal count of 3-4-4-4 and degenerate eyes (lacking retina and sometimes cornea).

ADDITIONAL DESCRIPTION.—Carapace with 1 pair of anterior tubercles. Penis typical for the group; ventral plate with strong apical setae and 6 pairs of lateral setae; stylus broad and flat,

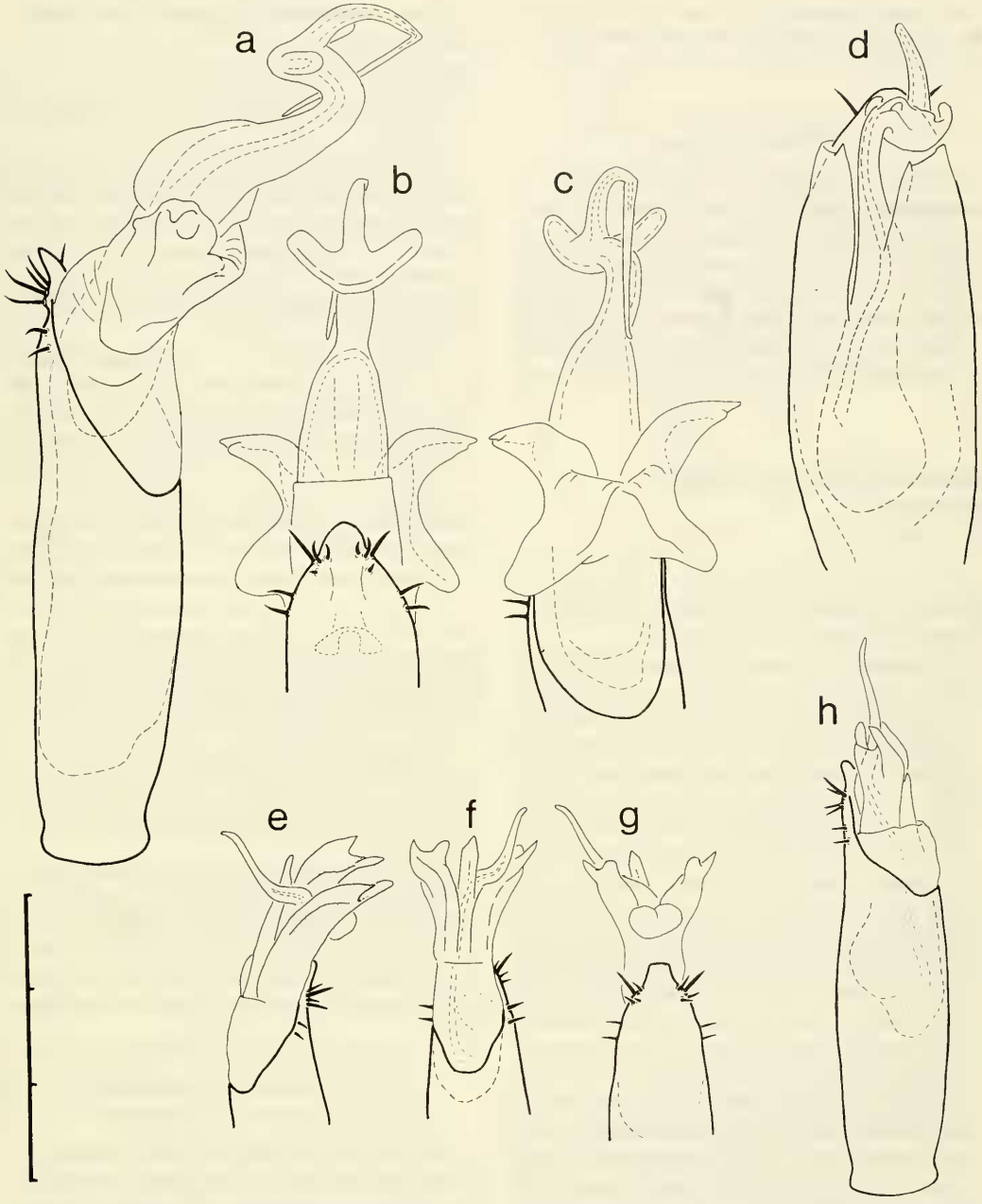


FIGURE 10. Male genitalia of the *arida* subgroup. (a–d) *C. cloughensis*. (a–c) Lateral, ventral, and dorsal views (topotype). (d) Dorsal view of slide-mounted specimen showing retracted glans (holotype). (e–h) *C. arida*. (e–g) Lateral, dorsal, and ventral views (holotype). (h) Sublateral view showing retracted glans (paratopotype).

parastyli very small. Ovipositor similar to that of *mariposa* but with 3 pairs of strongly reduced subapical setae and with sparse distribution of microspines.

TYPE SPECIMENS.—Male holotype and female allotype, under serpentine in marshy grassland at 0.8 mi (1.3 km) N Morro Bay, San Luis Obispo County, 2 Mar. 1967, VFL.

SPECIMENS EXAMINED.—Twenty-nine males, 25 females.

NEW RECORDS.—SAN LUIS OBISPO COUNTY: San Luis

Obispo, behind Madonna Inn, 22 Mar. 1970 (TSB, GL); 2.4 mi (3.9 km) NW San Simeon in serpentine grassland, 13 Feb. 1987 (TSB, VFL).

The *arida* Subgroup

DIAGNOSIS.—Members of this subgroup are distinguished from all other species by their unique glans penis: the stylus is strongly sinuous and the collar lobes are greatly enlarged. Males also lack spurs on their palpal tarsi but have enlarged mesobasal, spine-bearing tubercles.

DISTRIBUTION.—Known from a single locality in San Benito County and a cave in Tulare County.

Calicina arida Ubick and Briggs, new species
(Fig. 10e–h)

DIAGNOSIS.—Males of this paedomorphic species are unique in the genus in having the parastyli represented by a single rod.

ETYMOLOGY.—The specific name is a Latin adjective meaning dry, and refers to the climatic conditions in the vicinity of the type locality.

DESCRIPTION.—Color yellowish orange. Carapace with 1 pair of anterior tubercles. Retina absent, cornea present. Tarsal count 3-4-4-4.

Male: Total body length, 0.80. Scute length, 0.57. Scute width, 0.56. Eye tubercle length, 0.10. Eye tubercle width, 0.13. Leg II length, 1.65. Palpal tarsus without dorsal spur but with enlarged mesobasal spine-bearing tubercle. Penis relatively stout; ventral plate with slight apical attenuation and 6 pairs of setae; collar lobes greatly enlarged and apically directed; parastyli represented by a single, dorsal rod; stylus strongly sinuous and dorsally directed.

Female: Total body length, 0.73. Scute length, 0.50. Scute width, 0.53. Eye tubercle length, 0.06. Eye tubercle width, 0.08. Ovipositor with 12 apical setae, with 3 pairs of subapical setae and with a pair of short apical teeth; microspines sparsely distributed apically and laterally.

TYPE SPECIMENS.—Male holotype and 18 paratypes (nine males, nine females), under serpentine rocks in an oak gully at Panoche Road, 12.7 mi (20.4 km) SE Paicines, San Benito County, 1 Dec. 1984, TSB, VFL, and DU. One male paratopotype, 1 Dec. 1971, KH. Two paratypes (male, female) deposited at AMNH collection.

SPECIMENS EXAMINED.—Eleven males, 10 females.

Calicina cloughensis (Briggs and Hom, 1967), new combination
(Fig. 10a–d)

Sitalcina cloughensis Briggs and Hom, 1967:52. Briggs, 1968: 23.

DIAGNOSIS.—This species is the only troglobitic *Calicina* and is recognized by its pale coloration, complete loss of eyes (cornea as well as retina), and a high tarsal count (3-5-5-5). Furthermore, males of *cloughensis* have bilobed collar lobes and a unique stylus bearing a median enlargement.

ADDITIONAL DESCRIPTION.—Carapace with 1 pair of anterior tubercles. Penis with ventral plate bearing 6 pairs of lateral setae; collar lobes divided into apical and basal portions; stylus long and sinuous, with crescent-shaped enlargement at midlength, and with apical extension. Ovipositor with 12 apical setae (nine in one specimen) and 2 or 3 pairs of subapical setae; microspines sparsely distributed on lateral surface.

JUVENILES.—Two of the paratypes are early instar juveniles having tarsal counts of 1-2-2-2 and completely lacking eyes. Both lack anterior tubercles but have robust spines on the free tergites (adults have normal setae).

TYPE SPECIMENS.—Male holotype, female allotype, and six paratypes (male, three females, two juveniles), in Ladder Room of Clough Cave at South Fork Ranger Station 1,070 m (3,500 ft), Sequoia National Park, Tulare County, 14 May 1966, TSB, VFL, and KH.

SPECIMENS EXAMINED.—Four males, nine females, two juveniles.

NEW RECORDS.—TULARE COUNTY: Clough Cave, 18 Apr. 1979 (SW, EVI), 31 Aug. 1986 (TSB, KH, AKSJ).

REMARKS.—The stylus of the holotype male lacks the apical extension found in other specimens.

THE *PALAPRAEPUTIA* SPECIES GROUP
(The *palapraeputia* Subgroup)

DIAGNOSIS.—The single species representing this group has unique male genitalia: glans of penis three segmented with middle segment bearing a pair of hornlike collar lobes.

DISTRIBUTION.—Found only in Fresno County.

Calicina palapraeputia (Briggs, 1968), new combination
(Fig. 5e, f, 11, 16e, f)

Sitalcina palapraeputia Briggs, 1968:29.

DIAGNOSIS.—Same as for group.

ADDITIONAL DESCRIPTION.—Carapace with 2 or 3 pairs of anterior tubercles. Genital operculum with concave anterior margin. Penis with ventral plate truncate, apically elongated and armed with 7 pairs of setae; glans with two collars; collar lobes raptorial; stylus stout. Ovipositor with short distal segment, with 7 pairs of apical setae, and with a pair of large apical teeth; microspines present only at apex.

TYPE SPECIMENS.—Male holotype, female allotype, and six paratypes (three males, three females), under serpentine rocks in open grassland at 7 mi (11 km) NE Piedra, Fresno County, 21 Jan. 1967, TSB and KH.

SPECIMENS EXAMINED.—Fifteen males, 10 females.

NEW RECORDS.—FRESNO COUNTY: 10.2 mi (16.4 km) SW Trimmer, 27 Jan. 1968 (KH, JG); 8.7 mi (14 km) SW Trimmer, 27 Jan. 1968 (TSB, KH); 5.3 mi (8.5 km) SW Trimmer, 27 Jan. 1968 (TSB).

NATURAL HISTORY.—Found beneath serpentine and granite rocks in oak woodland and grassland biomes.

THE *SERPENTINEA* SPECIES GROUP

DIAGNOSIS.—Males of this group have a dorsal process on the glans penis. Females differ from those in the *digita* and *mariposa* groups in having an ovipositor with only apical microspines.

The *minor* Subgroup

DIAGNOSIS.—The morphology of the penis, dorsal process with ventrally directed basal lobes but no apical lobes, is diagnostic for the subgroup.

DISTRIBUTION.—Known only from San Mateo County.

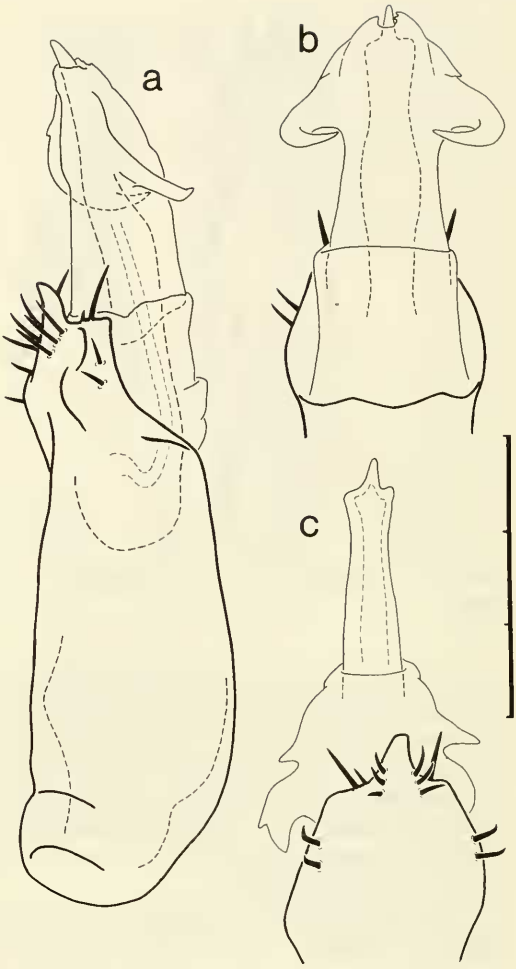


FIGURE 11. Male genitalia of *C. palapraeputia*. (a, b) Lateral and dorsal views showing partially expanded glans (5.3 mi SW Trimmer). (c) Ventral view showing fully expanded glans (10.2 mi SW Trimmer).

Calicina minor (Briggs and Hom, 1966), new combination

(Fig. 4c, 12)

Sitalcina minor Briggs and Hom, 1966:263. Briggs, 1968:27.

DIAGNOSIS.—This paedomorphic species is distinguished from all others by its unique glans penis: basal segment with transverse rows of small tubercles and dorsal process lacking apical lobes but with prominent basal lobes.

ADDITIONAL DESCRIPTION.—Carapace with at most 1 pair of anterior tubercles. Male palpal tarsus with enlarged mesobasal spine-bearing tubercle instead of spur. Penis with ventral plate apically produced and bearing 7 pairs of setae; dorsal process apically bifurcate, with ventrally directed basal lobes; stylus straight and tapering, basally thickened. Ovipositor with 6 pairs of apical and 3 pairs of subapical setae; microspines restricted to apex.

TYPE SPECIMENS.—Female holotype, male allotype, and four paratypes (one male, three females), under serpentine rocks on grassland hillside at 0.75 mi (1.2 km) N Crystal Springs Dam on County Road No. 14, San Mateo County, 23 Jan. 1966, TSB and KH.

SPECIMENS EXAMINED.—Twenty males, 23 females.

NEW RECORDS.—SAN MATEO COUNTY: Edgewood Park, serpentine grassland on N half of park, 2 Jan. 1983 (TSB, VFL, DU); 6 Apr. 1986 (TSB, TO); 2 Jan. 1987 (TSB, VFL, DU); 24 Dec. 1987 (TSB, VFL, WES, DU).

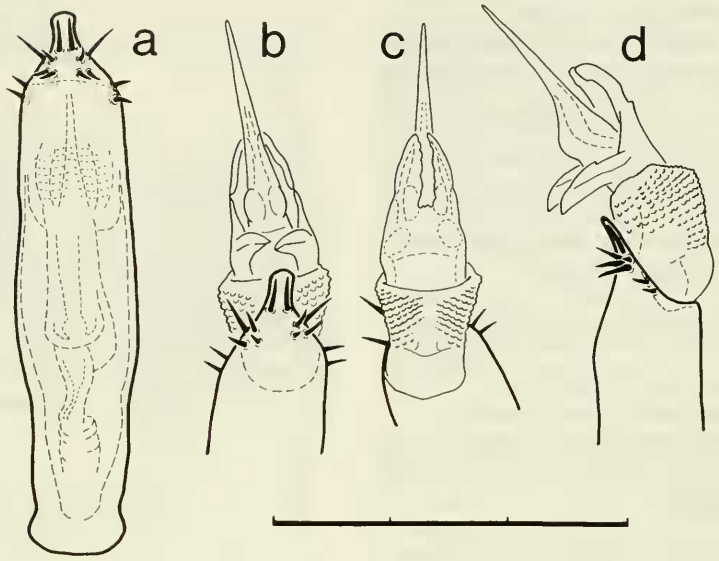


FIGURE 12. Male genitalia of *C. minor* (Edgewood Park). (a) Ventral view of penis shaft. (b–d) Ventral, dorsal, and lateral views.

DISTRIBUTION.—This species is presently known only from Edgewood Park. No specimens have been collected at the type locality (despite repeated attempts) since the completion of the adjacent highway. Also, the series of collections from Santa Clara County listed by Briggs and Hom (1966) represent an undescribed species belonging to a related genus.

NATURAL HISTORY.—All collections are from serpentine grassland.

The *serpentinea* Subgroup

DIAGNOSIS.—This subgroup, the largest in *Calicina,* includes those species whose males have a glans with a ventral stylus and a dorsal process bearing five apical lobes. The palpal spur, when present, is small or vestigial.

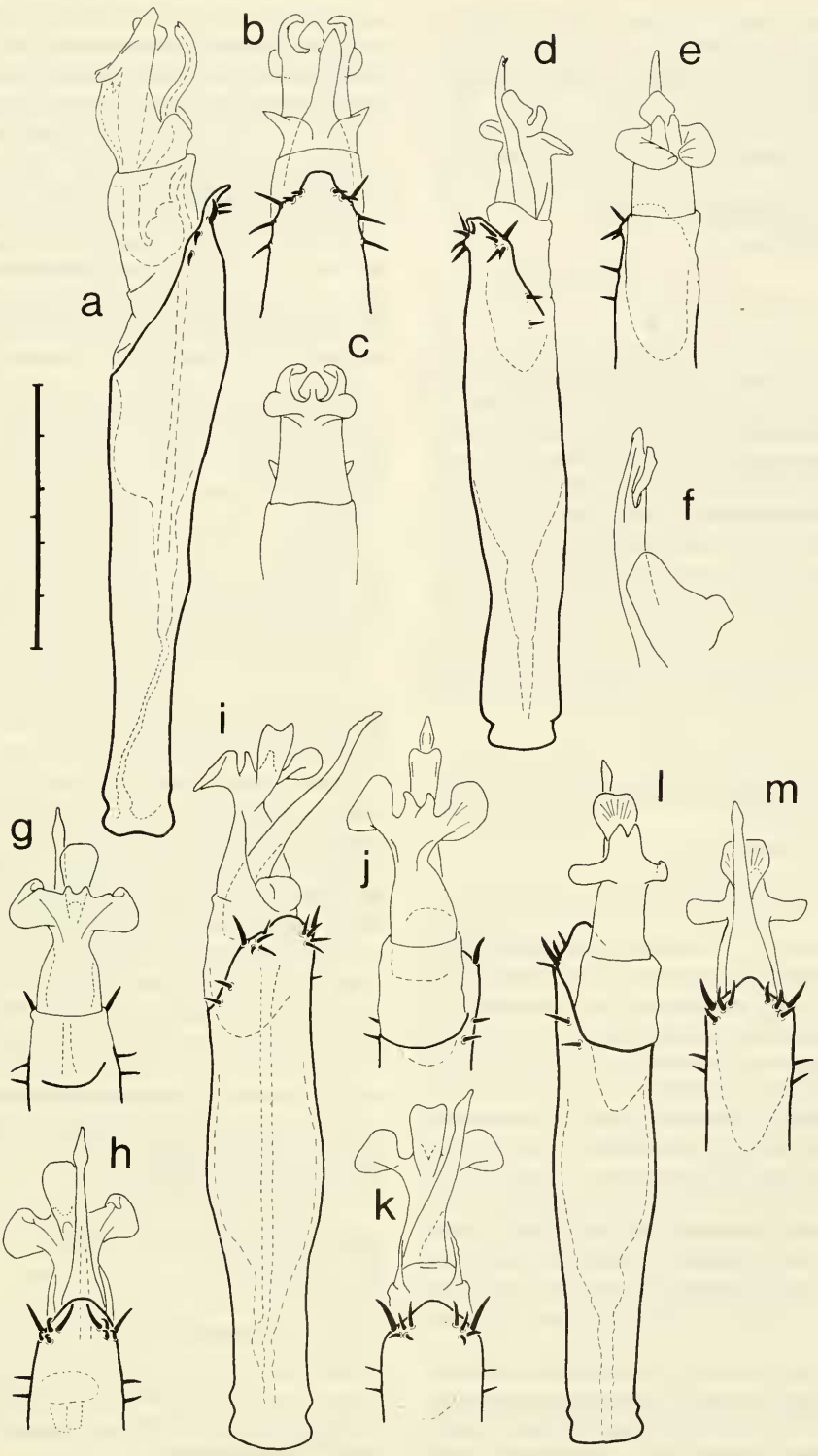
DISTRIBUTION.—The subgroup has a disjunct distribution with two populations in the lower Sierra Nevada foothills and a third along the central and northern Coast Ranges.

Key to Males of the Species of the *serpentinea* Subgroup

1. Glans with a pair of basal lobes (Fig. 13a–c, 18) ..... *piedra*
– Glans without basal lobes (Fig. 13d–m, 14) 2
2. Stylus longer than dorsal process (Fig. 13d–m) 3
– Stylus shorter than dorsal process (Fig. 14) 5
3. Tarsal count 3-4-4-5 ..... *serpentinea*
– Tarsal count 3-4-4-4 4
4. Dorsal process with lateral lobes as long as wide (Fig. 13d–f) ..... *ensata*
– Dorsal process with lateral lobes longer than wide (Fig. 13l, m) ..... *polina*
5. Body with dark maculations ..... *macula*
– Body concolorous 6
6. Dorsal process with lateral lobes as long as wide (Fig. 14a–f) 7
– Dorsal process with lateral lobes longer than wide (Fig. 14j–l) 8

→

FIGURE 13. Male genitalia of the *serpentinea* subgroup. 1. (a–c) *C. piedra* (holotype), lateral, ventral, and dorsal views. (d–f) *C. ensata* (Tollhouse). (d, e) Ventrolateral and dorsal views. (f) Dorsolateral view of stylus tip. (g–k) *C. serpentinea.* (g, h) Dorsal and ventral views (Monte Vista). (i–k) Ventrolateral, dorsal, and ventral views (San Felipe Road). (l, m) *C. polina* (Novato), dorsolateral and ventral views. (Scale bar equals 0.25 mm, except for "f" where it equals 0.10 mm.)


a
b
c
d
e
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g
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m

7. Median lobe of dorsal process apically notched (Fig. 14d–f) ..... *basalta*
– Median lobe of dorsal process apically pointed (Fig. 14a–c) ..... *breva*
8. Tarsal count 3-4-4-5 ..... *dimorphica*
– Tarsal count 3-4-4-4 ..... *mesaensis*

Calicina piedra (Briggs, 1968), new combination

(Fig. 13a–c)

Sitalcina piedra Briggs, 1968:24.

Diagnosis.—This species, the largest of the *serpentinea* group, is easily distinguished by the structure of the male genitalia: dorsal process of glans subequal in length to stylus, with a pair of basoventral lobes, and with small apical lobes.

Additional Description.—Carapace with 2 or 3 pairs of anterior tubercles. Penis with ventral plate apically attenuated and with 5 pairs of lateral setae; stylus flat, broad, and sinuous. Ovipositor as in *minor* but without subapical setae.

Type Specimens.—Male holotype, female allotype, and female paratype, under rocks in an oak grassland at 1.6 mi (2.6 km) SW Piedra, Fresno County, 21 Jan. 1967, TSB, KH, and AJ.

Specimens Examined.—Only the type series.

Calicina serpentinea (Briggs and Hom, 1966), new combination

(Fig. 3b, 5g, h, 13g–k, 16g, h)

Sitalcina serpentinea Briggs and Hom, 1966:268. Briggs, 1968: 26.

Diagnosis.—This species differs from others in its group by the combination of a tarsal count of 3-4-4-5 and structure of the male genitalia (stylus longer than the dorsal process and median lobe narrow and elongated).

Additional Description.—Carapace with 2 or 3 pairs of anterior tubercles. Eyes variable, cornea present or absent. Tarsal spur of male palpi may be absent or extremely small. Penis with ventral plate bearing 7 pairs of setae; dorsal process with narrow median lobe (with or without an apical notch) and rounded lateral lobes. Ovipositor with apical microspines, with 6–8 pairs of apical setae, and with one pair of apical teeth.

Variation.—*Calicina serpentinea* is polymorphic with regard to several characters. Individuals from the three westernmost localities (dense forest biomes) lack corneas and tarsal spurs, which are present in the remaining populations (grassland and oak woodland biomes). The female from Monte Vista lacks the paired apical teeth on the ovipositor. In individuals from Santa Clara and Contra Costa counties, the median lobe is apically entire (Fig. 13g, h), in others it is apically notched (Fig. 13i–k).

Juveniles.—The two known juveniles, from Bob's Secret Cave, are middle instars having tarsal counts of 2-2-3-3. They lack anterior tubercles. As in adults from this locality, the eyes are completely reduced (lacking both retina and cornea) and the free tergites lack enlarged spines.

Type Specimens.—Female holotype, male allotype, and six paratypes (two males, four females), under serpentine in marshy grassland along Silver Creek Road, 5 mi (8 km) SE Tully Road, San Jose, Santa Clara County, 27 Feb. 1966, TSB and CF.

Specimens Examined.—Fifty-one males, 38 females, two juveniles, seven specimens of undetermined sex.

New Records.—SANTA CLARA COUNTY: Silver Creek Road, 3.6 mi (5.8 km) from San Felipe Road, 2 Jan. 1983 (TSB, VFL, DU); Silver Creek at San Felipe Reservoir, 27 Nov. 1966 (TSB, AKSJ); Monte Vista, near Permanente Quarry, 24 Mar. 1968 (TSB); Metcalf Road, 1.8 mi (2.9 km) N Hwy 101, 2 Jan. 1983 (TSB, VFL, DU). SANTA CRUZ COUNTY: Cave Gulch, Bob's Secret Cave, 6 May 1984 (TSB, VFL, DU); Cave Gulch, 18 June 1984 (TSB, DU). SAN BENITO COUNTY: Lone Tree Road, 8.6 mi (13.8 km) W Fairview Road, 27 Dec. 1984 (TSB, VFL, DU).

Distribution.—Known from the southern Bay Area from San Mateo and Contra Costa to San Benito counties.

Natural History.—This wide-ranging species occurs in a variety of habitats; most commonly beneath serpentine in grassland and oak woodland biomes, but also from redwood, broadleaf evergreen, and digger pine-oak associations. There is also one collection from a cave. Most specimens were taken from under serpentine, but some were also collected beneath limestone and sandstone rocks, and fallen bark. While more commonly collected during the rainy season, this species is apparently active throughout the year in mesic refugia.

Calicina polina (Briggs, 1968), new combination

(Fig. 13l, m)

Sitalcina polina Briggs, 1968:30.

Diagnosis.—A unique dorsal process with a cordate median lobe and narrow lateral lobes distinguishes males of this paedomorphic species from all other species.

ADDITIONAL DESCRIPTION.—Carapace with 1 or 2 pairs of anterior tubercles. Penis with stylus longer than dorsal process; ventral plate with 6 pairs of setae. Ovipositor with 7 pairs of apical setae; microspines apical.

TYPE SPECIMENS.—Male holotype, female allotype, and three paratypes (two males, one female), under serpentine rocks in a moist grassland at El Polin Spring, Presidio, San Francisco County, 11 Dec. 1966, TSB.

SPECIMENS EXAMINED.—Forty-six males, 31 females, one specimen of undetermined sex.

NEW RECORDS.—SAN FRANCISCO COUNTY: Presidio Golf Course, 9 Nov. 1975 (TSB). MARIN COUNTY: 1 mi (1.6 km) NW Novato, 2 Apr. 1967 (TSB); Marin Dell Ranch, near Novato, 2 Jan. 1972 (TSB, AK); Novato, San Marin Drive, 7 Mar. 1982 (TSB, DU), 14 Mar. 1982 (DU); Novato, W of Burdell Mountain, 100 m (350 ft), 2 Jan. 1986 (TSB, DU); Novato, SW of Burdell Mountain, 170 m (550 ft), 2 Jan. 1986 (TSB, DU). SONOMA COUNTY: 2.5 mi (4 km) E Shellville, 2 Apr. 1967 (TSB); ALAMEDA COUNTY: Cull Canyon Road, 1 km N Crow Canyon Road, 22 Jan. 1984 (TSB, DU); Cull Canyon Road, 1.5 mi (2.4 km) N Crow Canyon Road, 22 Jan. 1984 (TSB, DU); Woolsey Canyon, Berkeley, 21 Dec. 1983 (TSB, VFL, DU); Redwood Road, 3.1 mi (5 km) N Castro Valley Road, 22 Jan. 1984 (TSB, DU); Chabot Reservoir at Lake Chabot Road, 6 Apr. 1982 (TSB, DU). CONTRA COSTA COUNTY: Wildcat Canyon Park near Hill Road, 30 Jan. 1984 (TSB), 14 July 1984 (TSB).

DISTRIBUTION.—This species is found in the northern part of the San Francisco Bay Region, from Sonoma south to San Francisco and Alameda counties.

NATURAL HISTORY.—The collections of *polina* west of San Francisco Bay (Sonoma, Marin, and San Francisco counties) are from serpentine grassland, whereas those from the East Bay are from beneath sandstone in oak forests.

Calicina ensata (Briggs, 1968), new combination
(Fig. 4d, 13d–f)

Sitalcina ensata Briggs, 1968:21.

DIAGNOSIS.—Males of this paedomorphic species may be distinguished from others in the subgroup in having a stylus which is longer than the dorsal process and has an apical prong.

ADDITIONAL DESCRIPTION.—Carapace with 2 or 3 pairs of anterior tubercles. Penis with ventral plate bearing 7 pairs of lateral setae; dorsal process with large lateral lobes; stylus long, tapering. Ovipositor with 12 apical setae and 3 pairs of subapical setae; microspines apical.

TYPE SPECIMENS.—Male holotype, female allotype, and 10 paratypes (eight males, two females), under rhyolite in an oak woodland at 2.0 mi (3.2 km) NW Trimmer, Fresno County, 16 Apr. 1967, TSB.

SPECIMENS EXAMINED.—Sixteen males, seven females.

NEW RECORD.—FRESNO COUNTY: W entrance to Watts Valley, 28 Jan. 1968 (TSB).

NATURAL HISTORY.—This species is known from oak woodland and has been collected beneath granite, rhyolite, and serpentine rocks.

Calicina macula (Briggs, 1968), new combination
(Fig. 14g–i)

Sitalcina macula Briggs, 1968:23.

DIAGNOSIS.—This is the only *Calicina* with a dark marbled color pattern. Males of this paedomorphic species may also be distinguished by the proportions of the dorsal process lobes and in having enlarged mesoapical spine-bearing tubercles on male palpal tarsi.

ADDITIONAL DESCRIPTION.—Carapace with 2 pairs of anterior tubercles. Penis typical for the *serpentinea* group; dorsal process with notched median lobe; ventral plate with 7 pairs of lateral setae. Ovipositor with 12 apical and 3 pairs of subapical setae; microspines apical.

TYPE SPECIMENS.—Male holotype, female allotype, and nine paratypes (eight males, one female), under serpentine rocks in an oak grassland at 9 mi (14.5 km) SE Academy, Fresno County, 16 Apr. 1967, TSB.

SPECIMENS EXAMINED.—Only the type series.

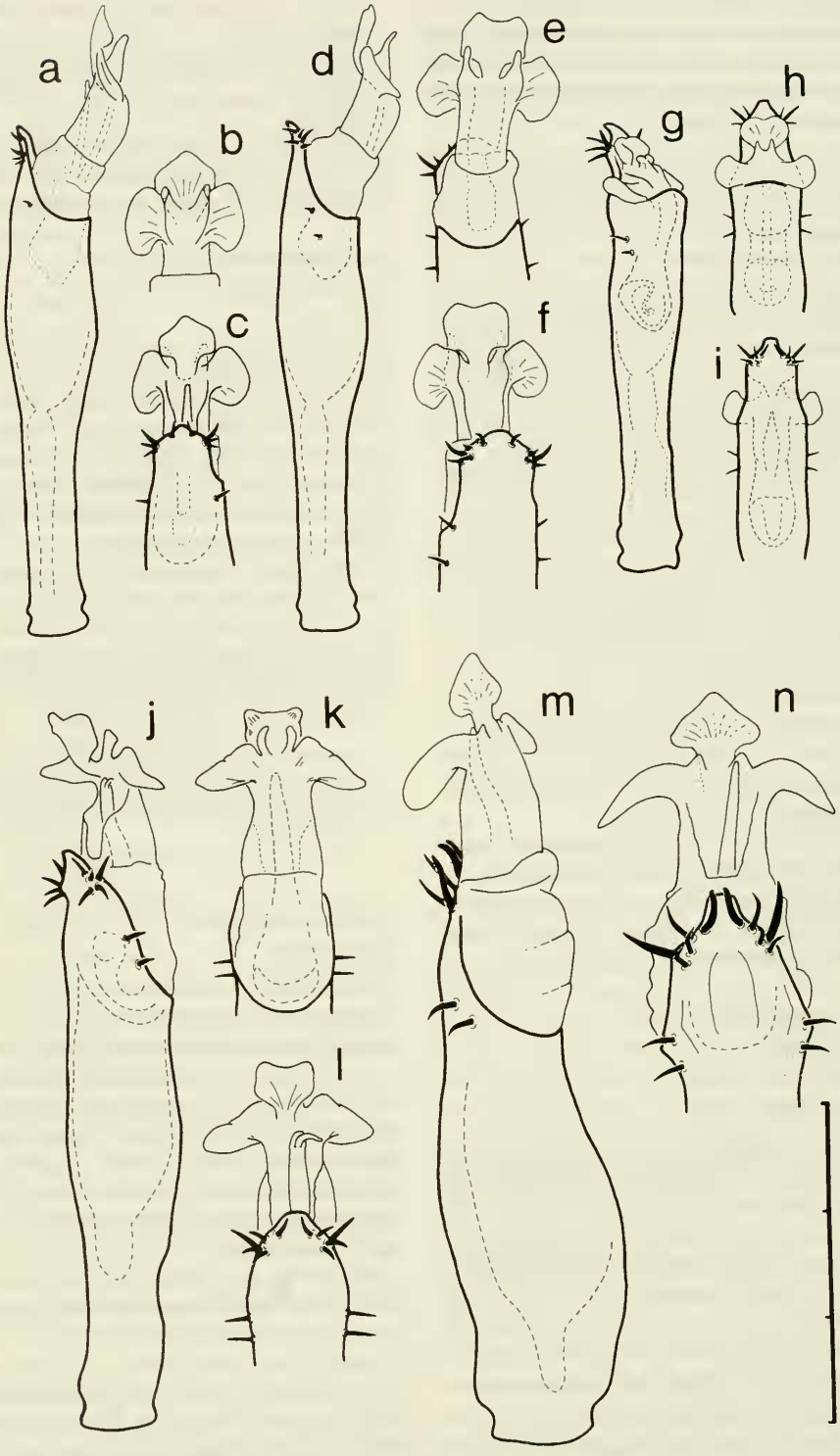
Calicina dimorphica Ubick and Briggs, new species
(Fig. 14m, n)

DIAGNOSIS.—Males of this species are distinguished from all others in the group in having a dorsal process with a diamond-shaped central lobe and elongated lateral lobes. Males lack the palpal spur but have an enlarged mesoapical spine-bearing tubercle on the palpal tarsus.

ETYMOLOGY.—The specific name refers to the sexually dimorphic palpal spination characteristic of this species.

DESCRIPTION.—Color yellowish orange. Carapace with 3 pairs of anterior tubercles. Eyes well developed. Tarsal count 3-4-4-5.

Male: Total body length, 1.22. Scute length, 0.86. Scute width, 0.90. Eye tubercle length, 0.17. Eye tubercle width, 0.18. Leg II length, 2.07. Palpal tarsus without dorsal spur but with enlarged mesoapical spine-bearing tubercle. Penis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with ventral plate bearing 7 pairs of setae, of which 2 distal pairs are enlarged. Dorsal process with long, tapering lateral lobes and diamond-shaped median lobe.

Female: Total body length, 1.00. Scute length, 0.63. Scute width, 0.60. Eye tubercle length, 0.13. Eye tubercle width, 0.12. Palpal tarsus without enlarged spine-bearing tubercle. Ovipositor with apical microspines, 12 apical setae, and 1 pair of subapical setae.

TYPE SPECIMENS.—Male holotype and three paratypes (two males, one female) under granite in an oak grassland at the NE entrance to Watts Valley, Fresno County, 28 Jan. 1968, TSB.

SPECIMENS EXAMINED.—Only the type series.

Calicina mesaensis Ubick and Briggs, new species
(Fig. 4b, 14j–l)

DIAGNOSIS.—Males of this paedomorphic species differ from all others in having a dorsal process with a quadrate median lobe and elongate lateral lobes.

ETYMOLOGY.—The specific name is a reference to the type locality, Table Mountain.

DESCRIPTION.—Color yellow-orange. Carapace with 2 pairs of anterior tubercles. Eyes well developed. Tarsal count 3-4-4-4.

Male: Total body length, 1.14. Scute length, 0.87. Scute width, 0.82. Eye tubercle length, 0.18. Eye tubercle width, 0.17. Leg II length, 2.02. Palpal tarsus with greatly reduced dorsal spur (Fig. 4b). Penis with 7 pairs of setae on ventral plate. Dorsal process with quadrate median lobe and tapering lateral lobes. Stylus with apical prong.

Female: Total body length, 1.13. Scute length, 0.78. Scute width, 0.71. Eye tubercle length, 0.15. Eye tubercle width, 0.13. Ovipositor with apical microspines and 7 pairs of apical setae.

TYPE SPECIMENS.—Male holotype and 25 paratypes (11 males, 14 females), under basalt rocks in an oak grassland at Table Mountain, 2.8 mi (4.5 km) N Millerton Lake Road on Sky Harbor Road, Fresno County, 31 Mar. 1985, TSB, TO, WCR, and DU. Two paratypes (male, female) deposited at the AMNH collection.

SPECIMENS EXAMINED.—Only the type series.

Calicina breva (Briggs, 1968), new combination
(Fig. 14a–c)

Sitalcina sierra breva Briggs, 1968:21.

DIAGNOSIS.—Males of this paedomorphic species may be distinguished by the structure of the dorsal process: median lobe pentagonal, subequal to the laterals, and ventral plate with only 5 pairs of setae.

ADDITIONAL DESCRIPTION.—Carapace with 1 or 2 pairs of anterior tubercles. Penis with ventral plate bearing 5 pairs of small setae; dorsal process with three subequal, cloverlike lobes; stylus short and straight. Ovipositor with apical microspines and 7 pairs of apical setae.

TYPE SPECIMENS.—Male holotype, female allotype, and five paratypes (three males, two females), under basalt rocks in a grassland at 1 mi (1.6 km) S Knight's Ferry, Stanislaus County, 11 Apr. 1967, TSB.

SPECIMENS EXAMINED.—Only the type series.

Calicina basalta Ubick and Briggs, new species
(Fig. 14d–f)

DIAGNOSIS.—This paedomorphic species is most closely related to *breva* from which it may be distinguished by the notched median lobe of the dorsal process of the penis.

ETYMOLOGY.—The specific name refers to the microhabitat of this species.

DESCRIPTION.—Color yellow. Carapace with 1 or 2 pairs of anterior tubercles. Retina occasionally absent. Tarsal count 3-4-4-4.

Male: Total body length, 1.08. Scute length, 0.70. Scute width, 0.77. Eye tubercle length, 0.13. Eye tubercle width, 0.15. Leg II length, 2.07. Palpal tarsus without dorsal spur. Penis similar to that of *breva* except that dorsal lobe has notched median lobe.

Female: Total body length, 0.86. Scute length, 0.60. Scute width, 0.63. Eye tubercle length, 0.12. Eye tubercle width, 0.12. Ovipositor with apical microspines and 7 pairs of apical setae.

←

FIGURE 14. Male genitalia of the *serpentinea* subgroup. 2. (a–c) *C. breva* (paratopotype), lateral, dorsal, and ventral views. (d–f) *C. basalta* (holotype), lateral, dorsal, and ventral views. (g–i) *C. macula* (holotype), sublateral, dorsal, and ventral views showing retracted glans. (j–l) *C. mesaensis* (holotype), lateral, dorsal and ventral views. (m, n) *C. dimorphica* (paratopotype), lateral and ventral views.

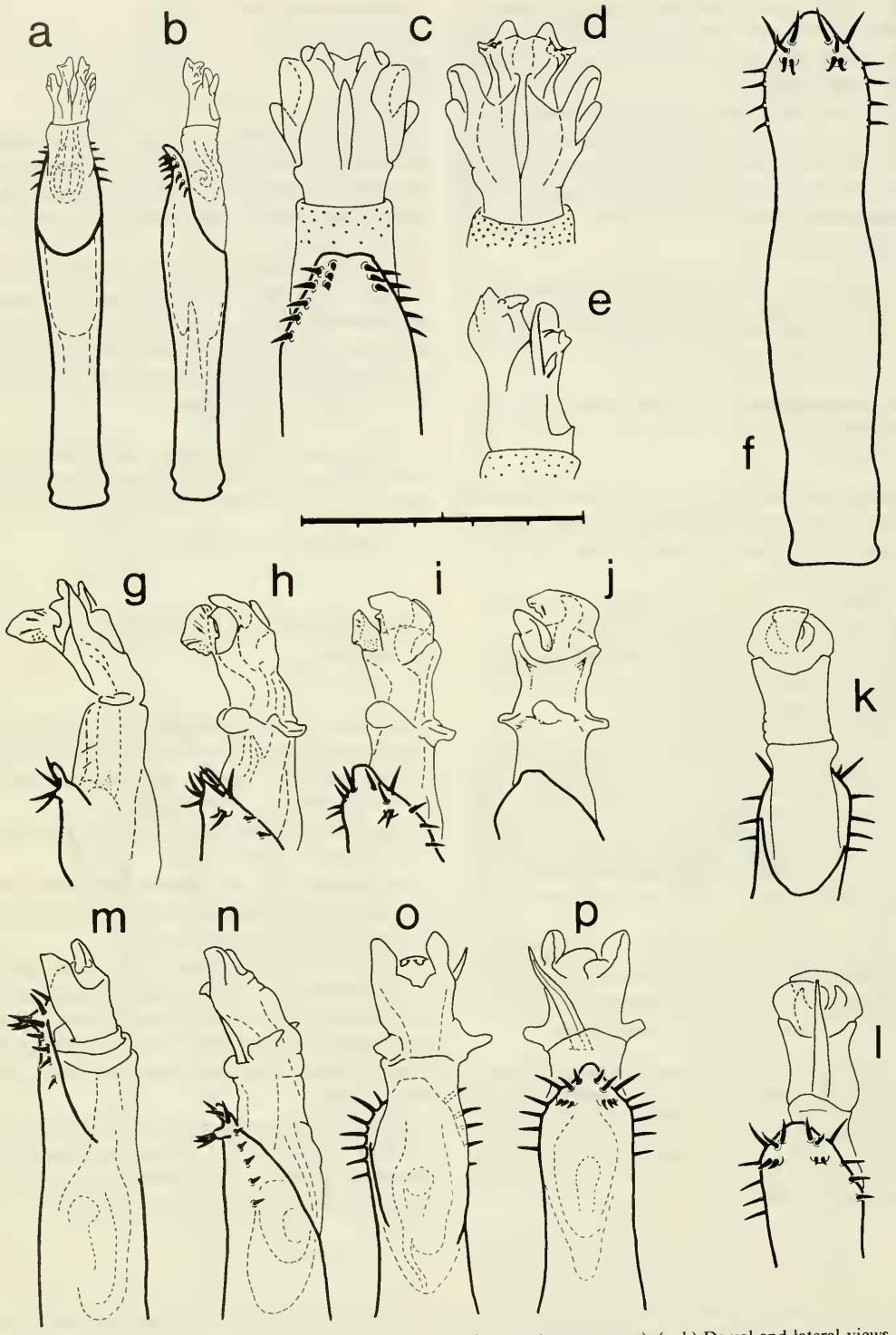

FIGURE 15. Male genitalia of the *sequoia* subgroup. (a–e) *C. diminua* (paratopotype). (a, b) Dorsal and lateral views. (c–e) Ventral, dorsal, and lateral views. (f–p) *C. sequoia*. (f) Ventral view of penis, truncus (Little River). (g–j) Lateral to ventral views (Little River). (k, l) Dorsal and ventral views (Pine Ridge Road). (m) Lateral view showing retracted glans (Mendocino). (n–p) Lateral, dorsal, and ventral views (Usal Creek). (Scale bar equals 0.25 mm, except for "c–e" where it equals 0.10 mm).

TYPE SPECIMENS.—Male holotype and five paratypes (three males, two females), under basalt rocks in a grassland area 8 mi (12.9 km) SW Jamestown, Tuolumne County, 10 Feb. 1968, TSB. Six paratypes (three males, three females) taken in similar conditions at 13 mi (21 km) E Oakdale, Stanislaus County, 10 Feb. 1968, TSB and BL.

SPECIMENS EXAMINED.—Seven males, five females.

The *sequoia* Subgroup

DIAGNOSIS.—The presence of at least 5 pairs of regularly spaced lateral setae on the ventral plate and the extremely complex dorsal process are diagnostic for this subgroup.

DISTRIBUTION.—Known from the northern Coast Ranges of California.

Calicina diminua Ubick and Briggs, new species
(Fig. 15a–e)

DIAGNOSIS.—This paedomorphic species, the smallest *Calicina,* is most easily distinguished by the elaborate structure of the glans penis.

ETYMOLOGY.—The specific name is a reference to the small size of this species.

DESCRIPTION.—Color yellow. Carapace without anterior tubercles. Eyes, both retina and lens, absent. Tarsal count 3-4-4-4.

Male: Total body length, 0.77. Scute length, 0.49. Scute width, 0.53. Eye tubercle length, 0.08. Eye tubercle width, 0.09. Leg II length 1.41. Palpal tarsus with dorsal spur. Penis small; ventral plate with 5 pairs of lateral setae and two triads of ventral setae; dorsal process ornate; stylus short and spinelike.

Female: Total body length, 0.60. Scute length, 0.46. Scute width, 0.46. Eye tubercle length, 0.06. Eye tubercle width, 0.07. Ovipositor with only 10 apical setae and without subapical setae or microspines.

TYPE SPECIMENS.—Male holotype and 11 paratypes (four males, seven females), under serpentine on a grassland hillside at Novato, San Marin Drive, Marin County, 2 Jan. 1986, TSB and DU. Five paratypes, 0.5 km SW of type locality, 7 Dec. 1985 (male) and 28 Apr. 1968 (three males, one female), TSB. Two paratypes (male, female) deposited at the AMNH collection.

SPECIMENS EXAMINED.—Nine males, eight females.

Calicina sequoia (Briggs and Hom, 1966), new combination
(Fig. 15f–p)

Sitalcina sequoia Briggs and Hom, 1966:267. Briggs, 1968:28.

DIAGNOSIS.—In addition to their distinctive male genitalia (dorsal process large with 1 or 2 pairs of lobes and ventral plate with 6 to 8 pairs of lateral setae) these small phalangodids have the most reduced tarsal count of any *Calicina* (3-4-4-4 or less), but unlike most other paedomorphic species, have well developed eyes.

ADDITIONAL DESCRIPTION.—Tarsal count usually 3-3-4-4, occasionally 3-4-4-4. Carapace with 1 pair of anterior tubercles. Penis with ventral plate bearing 6–8 pairs of lateral setae and 2 or 3 pairs of ventral setae; dorsal process with two pairs of lobes (the basal pair sometimes missing) and an apical portion capable of hyperextension; stylus ventral, spinelike. Ovipositor with apical microspines, 6 pairs of apical setae, 2 pairs of subapical setae, and 1 pair of apical teeth.

VARIATION.—The five specimens from the southernmost localities (Pine Ridge Road and Talmage) have the higher tarsal count of 3-4-4-4 and lack dorsobasal lobes on the dorsal process (Fig. 15k, l) but, otherwise, do not differ in genitalic features.

JUVENILES.—The only known juvenile, from Mendocino, is an early instar having a tarsal count of 1-1-2-2. As in adults, the eyes are well developed. However, the anterior tubercles are absent and the free tergites are armed with robust spines which are absent in adults.

TYPE SPECIMENS.—Female holotype, male allotype, and six paratypes, under rocks and logs in a Douglas fir forest at 2.3 mi (3.7 km) S Piercy, Mendocino County, 13 Mar. 1966, TSB and KH.

SPECIMENS EXAMINED.—Twenty-two males, 24 females, one juvenile, seven specimens of undetermined sex.

NEW RECORDS.—MENDOCINO COUNTY: 2.3 mi (3.7 km) S Piercy, 17–18 June 1966 (KH, VFL); Mendocino, 4 May 1963 (DCR); 5 mi (8 km) S Usal Creek, 17 Apr. 1976 (TSB); Pine Ridge Road, 1.6 mi (2.6 km) S Low Gap Road, W of Ukiah, 10 Feb. 1985 (TSB); Casper, 3 Aug. 1957 (JRH, GAM; AMNH collection); Talmage, 29 July 1959 (LMS, ROS; UCB collection).

NATURAL HISTORY.—This species is known from redwood and Douglas fir forests and has been collected beneath both logs and rocks. Six samples contained individuals of "*Sitalcina*" *cockerelli* Goodnight and Goodnight.

PHYLOGENY

MONOPHYLY OF *CALICINA*

Calicina is believed to be monophyletic on the basis of its unique palpal tarsus and possible synapomorphies in the ovipositor and glans morphologies. Among the Nearctic phalangodids, only the species of *Calicina* have a telescoping

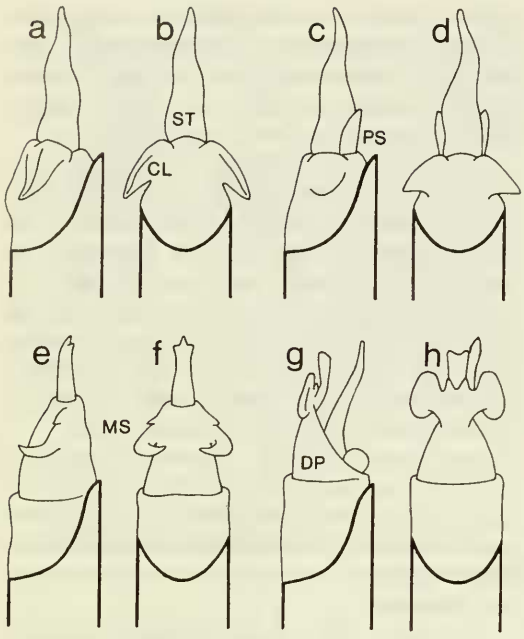

FIGURE 16. *Calicina*, glans types (a, c, e, g = lateral views; b, d, f, h = dorsal views). (a, b) *C. mariposa*, ST = stylus, CL = collar lobe. (c, d) *C. digita*, PS = parastylus. (e, f) *C. palapraeputia*, MS = middle segment. (g, h) *C. serpentinea*, DP = dorsal process.

glans (Fig. 16). Representatives of all other nominal genera were examined and found to have a folding glans. At this time it is not possible to determine which of these character states is derived. Outgroup comparison cannot be used since the sister group of these (presumably closely related) genera is not known. It may be argued that the folding glans, because of its widespread occurrence, is plesiomorphic. However, the telescoping glans is functionally simpler, whereas the folding glans is usually associated with other derived genital characters, such as the bifurcate ventral plate of *Banksula* Roewer, *Texella* Goodnight and Goodnight, and all Appalachian genera.

The tarsal spur is not known in any other phalangodid genus and is, clearly, a synapomorphy for *Calicina* (Fig. 17, component 1). However, several species that we include in *Calicina* lack the spur, which we interpret to be the result of a character reversal. The tarsal spur is most strongly developed in the two least derived taxa of *Calicina* (the *mariposa* group and the *digita* subgroup) but is reduced in size or absent in most of the remaining species. Of the 11 species that completely lack the spur, most are closely related (based on genitalic characters) to species having distinct, but small, spurs (the seven species belonging to the *kaweahensis, serpentinea,* and *sequoia* subgroups). Likewise, on the basis of their glans structure, the two species in the *arida* subgroup and the monotypic *minor* subgroup are clearly representatives of the *digita* and *serpentinea* species groups, respectively. This leaves only one unassociated species, *palapraeputia,* that lacks the spur. However, despite the unique glans structure of this species, its generic placement is not questioned because, in addition to having a telescoping glans, its ovipositor closely resembles that of some *Calicina* species in microspine distribution and setal arrangement (compare Fig. 5e, f and 5g, h).

The ovipositor of *Calicina* differs from that of *Sitalcina* in several characters (Table 1). Of these, microspines may be derived because, with few exceptions, they do not occur in other Californian phalangodid species. Also, two setal series (apical and subapical) present in most *Calicina* species have not been observed in *Sitalcina* nor in other Californian phalangodid genera. Further investigation will be necessary to determine the polarities of these character states and their universality.

Sister Group

There are two possible sister groups of *Calicina.* The first consists of the genera which have a telescoping glans. Of the European phalangodids, apparently only *Ptychosoma* Soerensen has this type of glans (see figures in Brignoli 1968). Two additional species with telescoping glans have recently been described in *Scotolemon* Lucas (*espanoli* Rambla, 1973 and *balearicus* Rambla, 1977) but, based on the published genital illustrations, appear to be congeneric with *Ptychosoma.* Although similar to *Calicina* in general body structure, *Ptychosoma* differs in having a greater number of palpal spine-bearing tubercles, in having a strongly modified ventral plate, and in lacking sexually dimorphic structures.

A telescoping glans is likewise found in some Southeast Asian genera. *Buparellus* Roewer and *Bupares* Thorell have a glans structure quite similar to some *Calicina* species, but they differ in having more strongly armed palpi (see figures in Suzuki 1985). The Japanese *Parabeloniscus* Su-

TABLE 2. LIST OF CHARACTERS AND THEIR PRESUMED POLARITIES.

Character	Plesiomorphic	Apomorphic
1. male palpal tarsus	unmodified	with spur
2. parastylus	absent	present
3. stylus shape	sinuous	straight
4. parastylus insertion	ventral	(a) lateral, (b) dorsal
5. microspine distribution	distal half of ovipositor	restricted to apex
6. glans segments	two	three
7. dorsal process (DP)	absent	present
8. DP apex	bifurcate	lobate
9. basoventral lobes of DP	present	absent
10. median lobe length	shorter than paramedian lobes	longer than paramedian lobes
11. stylus length	subequal to DP	(a) longer than DP (b) shorter than DP
12. lateral lobe shape	length = width	length > width

zuki shares with *Calicina* a similar glans and ventral plate spination but has increased palpal spination and a sexually dimorphic third tergite (elongated in males) (see figures in Suzuki 1973). Although placed in the Phalangodinae, these genera also lack the characteristic eye tubercle and may belong elsewhere.

Finally, the genitalia of Assamiidae and Biantidae strongly resemble those of some *Calicina* species (see figures in Martens 1977, 1986). Members of these families, however, have highly modified palpi (segments are elongated and attenuated and spination is reduced) and generally lack well defined eye tubercles.

The relationship of *Calicina* to the above taxa depends on the phylogenetic significance of the telescoping glans. If this glans structure is derived, then these and additional taxa may actually be closely related. On the other hand, if the telescoping state is plesiomorphic, then differences in somatic characters assume greater importance. In this case, the somatically similar Californian phalangodids become the second group of potential candidates for the *Calicina* sister group. Of these, the most likely possibility is a recently discovered (and undescribed) phalangodid genus that has a glans that unfolds *and* telescopes during expansion. This relationship will be explored in a future study.

Intrageneric Relationships

The proposed relationships among the *Calicina* species are based primarily on the male genitalia. The characters used, along with their presumed polarities, are given in Table 2 and the resulting cladograms are presented in Figures 17 and 18.

As described earlier, four types of glans occur in *Calicina*. These appear to define the major lineages that are here recognized as species groups. Each group is defined by unique structures or character states, interpreted as autapomorphies: the *mariposa* group by dorsally grooved collar lobes, the *digita* group by parastyli, the *palapraeputia* group by an additional glans segment, and the *serpentinea* group by a dorsal process (Fig. 16).

The *mariposa* group contains species with the simplest glans morphology (Fig. 6, 16a, b). This glans contains two segments: the basal bears a pair of collar lobes and the apical consists of a sinuous stylus. This structural simplicity is assumed to be plesiomorphic. The presence of plesiomorphic somatic characters in this group is at least consistent with this interpretation. First, *Calicina mariposa* has a tarsal count of 3-5-5-5. With the exception of a few species in the *digita* group, all other *Calicina* species have lower counts. High tarsal counts, 3-5-5-5 or higher, occur in virtually all other Holarctic phalangodids. Second, the males of all species in the *mariposa* group have well developed tarsal spurs. This state, as argued previously, is presumed to be plesiomorphic within the genus.

The glans in the *digita* group is similar to that in the *mariposa* group, but contains an additional pair of sclerites, the parastyli (PS) (Fig. 16c, d, component 2). The *digita* subgroup has ventral, scalelike parastyli and a sagittate ventral plate (Fig. 7). It is the most generalized element of the group because it retains the high tarsal count,

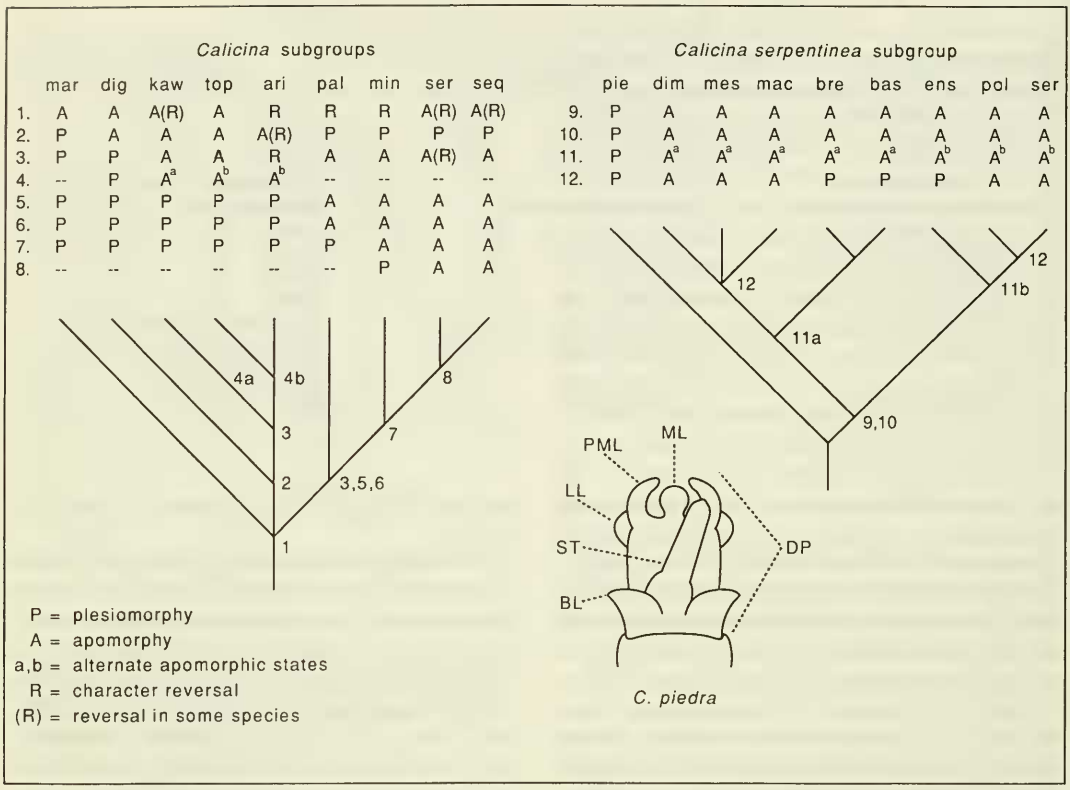

FIGURE 17. Cladogram with data matrix showing the relationships of *Calicina* subgroups using characters given in Table 2. Abbreviations: mar = *mariposa*, dig = *digita*, kaw = *kaweahensis*, top = *topanga*, ari = *arida*, pal = *palapraeputia*, min = *minor*, ser = *serpentinea*, and seq = *sequoia*.

FIGURE 18. Cladogram with data matrix showing the relationships of species in the *serpentinea* subgroup using characters given in Table 2. The drawing is the glans, ventral view, of *C. piedra*. Abbreviations: pie = *piedra*, dim = *dimorphica*, mes = *mesaensis*, mac = *macula*, bre = *breva*, bas = *basalta*, ens = *ensata*, pol = *polina*, ser = *serpentinea*, DP = dorsal process, ML = median lobe, PML = paramedian lobe, LL = lateral lobe, BL = basal lobe, and ST = stylus.

well developed tarsal spurs, and a *mariposa*-like sinuous stylus. The stylus of the *kaweahensis* and *topanga* subgroups is straight, and considered to be derived (component 3). In the former, the PS are broad, ornate, and laterally inserted (Fig. 8, component 4a). In the *topanga* subgroup the PS are rodlike and inserted dorsolaterally to the stylus (Fig. 9). The two species of the *arida* subgroup have an unusual glans morphology for their group (Fig. 10). In *arida* the PS are represented by a single dorsal rod, whereas in *cloughensis* they are totally absent. Despite the absence of PS, *cloughensis* is undoubtedly a member of this subgroup because of its close relationship with *arida*. (See the diagnosis of the subgroup for synapomorphies.) Using the *digita* subgroup as an outgroup, the dorsal position of the PS in the *arida* and *topanga* subgroups is synapomorphic (component 4b).

Calicina palapraeputia, the sole representative of its group, differs from all other *Calicina* species in having a three-segmented glans (Fig. 11, 16e, f). If the stylus and basal segment of this glans are homologous to comparable parts of the *mariposa* glans, the middle segment is left unassociated. One possibility is that this segment represents a highly modified PS that enveloped and fused around the stylus, as appears to occur in *kaweahensis* (Fig. 8e–g). Alternatively, the middle segment could have developed from similarly modified collar lobes from an *arida*-like ancestor (Fig. 10e–h). Either of these mechanisms would probably be accompanied by the fusion of these structures (PS or collar lobes) on the middle segment, but no evidence of this has been detected. Furthermore, both interpretations require the independent acquisition of the middle segment

lobes in *palapraeputia.* A more parsimonious alternative (and the one we accept) is that the lobes in *palapraeputia* are actually collar lobes, homologous to those found in the *mariposa* and *digita* groups. In this case the *palapraeputia* glans could be derived from a *mariposa* type through the development of an additional collar on the basal segment of the latter.

In the *serpentinea* group the glans has a derived, lobe-bearing structure, the dorsal process (Fig. 16g, h, component 7). In most species (the *serpentinea* subgroup) the dorsal process (DP) bears five apical lobes (Fig. 13, 14). The remaining three species all have unique DP morphologies. *Calicina minor,* the sole representative of its subgroup, has the simplest DP bearing a pair of dorsobasal lobes and an apical bifurcation instead of lobes (Fig. 12). Of the members of the *sequoia* subgroup, the DP of *diminua* is divided into two lateral, extremely ornate, hemispheres; whereas in *sequoia* it contains a pair of basal and apical lobes in addition to a complex apical region (Fig. 15). Despite fundamental differences in the glans structure, the last two species seem to be related as they share a unique ventral plate spination. The presence of apical lobes on the DP appears to be a synapomorphy uniting all species of the *serpentinea* group except *minor* (component 8).

The species of the *serpentinea* subgroup all have rather similar glans morphologies, with the exception of *piedra.* The *piedra* glans differs from the others in four characters: (1) DP with basal lobes, (2) paramedian lobes longer than median lobe, (3) lateral lobes wider than long, and (4) stylus subequal to DP in length (Fig. 13a–c, 18). Because basal lobes are found in the other subgroups, their presence is a synapomorphy for the entire *serpentinea* group, but a plesiomorphy at the subgroup level. The implication that *piedra* is the most generalized species in the subgroup is compatible with its relatively higher tarsal count (3-4-4-5). The remaining species in this subgroup are united in lacking basal lobes (component 9) and in having relatively larger median lobes (component 10). They are subdivided into two groups based on stylus length. Using *piedra* as the outgroup, stylus lengths either longer (component 11a) or shorter (component 11b) than the DP appear to be synapomorphic. Finally, elongated lateral lobes (component 12) are synapomorphic for some species.

Because of the *serpentinea* group's unique glans morphology, its relationship to the other groups would appear remote. However, its ovipositor structure implies a close relationship with *palapraeputia.* In both groups the distribution of microspines is restricted to the apical surface of the ovipositor which, using *mariposa* as the outgroup, is synapomorphic (component 5). This relationship suggests that the glans morphologies in the two groups are likewise closely related; namely, that the dorsal process (DP) is homologous to the *palapraeputia* middle glans segment (component 6). The DP could conceivably have developed from the middle segment by the enlargement of the stylus opening along the ventroapical surface. In fact, the basal lobes of the DP, evident in members of all subgroups, may well be vestiges of the ventral surface of the middle segment.

Two alternative explanations for the origin of the DP are possible. First, the DP might represent highly derived parastyli. In *kaweahensis,* for example, the parastyli are greatly enlarged, partially envelop the stylus, and are fused dorsally (Fig. 8e–g). Further enlargement could result in a DP. However, this interpretation requires the concomitant loss of collar lobes in the *serpentinea* group. Second, the DP might be homologous to collar lobes. In *arida* the collar lobes are large and apically produced (Fig. 10e–h) and could conceivably form a DP through fusion and additional enlargement. However, this interpretation requires a character reversal of parastyli in the *serpentinea* group. Furthermore, both of these explanations imply a sister group relationship between the *serpentinea* group and either *kaweahensis* or *arida* which is not supported by any other known character.

Biogeography

As is to be expected of cryptozoic organisms having low dispersal potential, the species of *Calicina* are allopatric or parapatric (see Fig. 19). The four known instances of sympatry, between *palapraeputia* and *ensata, diminua* and *polina, digita* and *kaweahensis,* and *digita* and *cloughensis,* are all between members of different groups or subgroups. Furthermore, these cases of sympatry may not actually involve interspecific interaction. In the last case, for example, *cloughensis* is troglobitic and *digita* epigean. Also, though *diminua* and *polina* live in close prox-

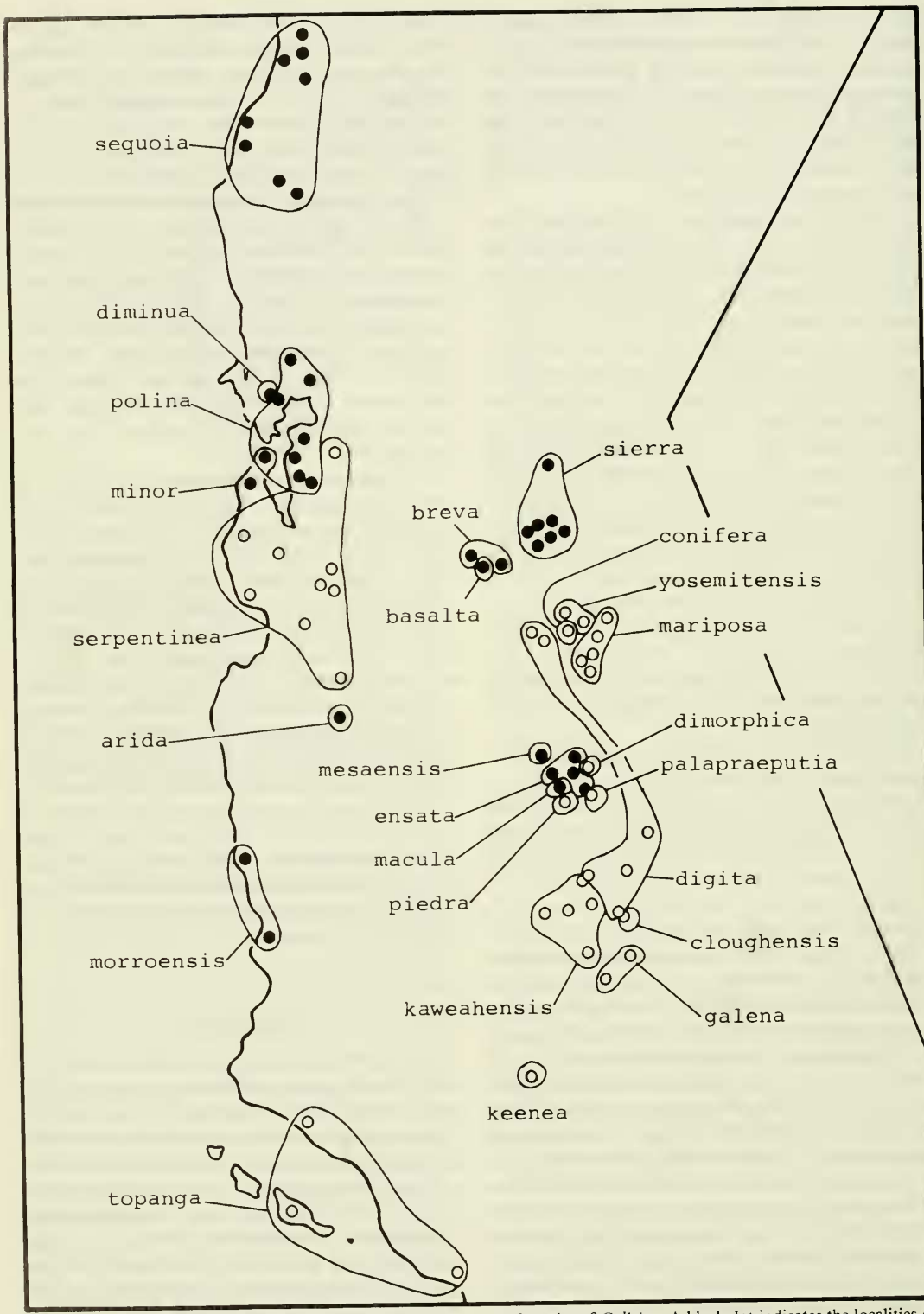

FIGURE 19. Map of central California showing the distribution of species of *Calicina*. A black dot indicates the localities of paedomorphic species, a circle those of non-paedomorphics. Overlapping symbols denote sympatry.

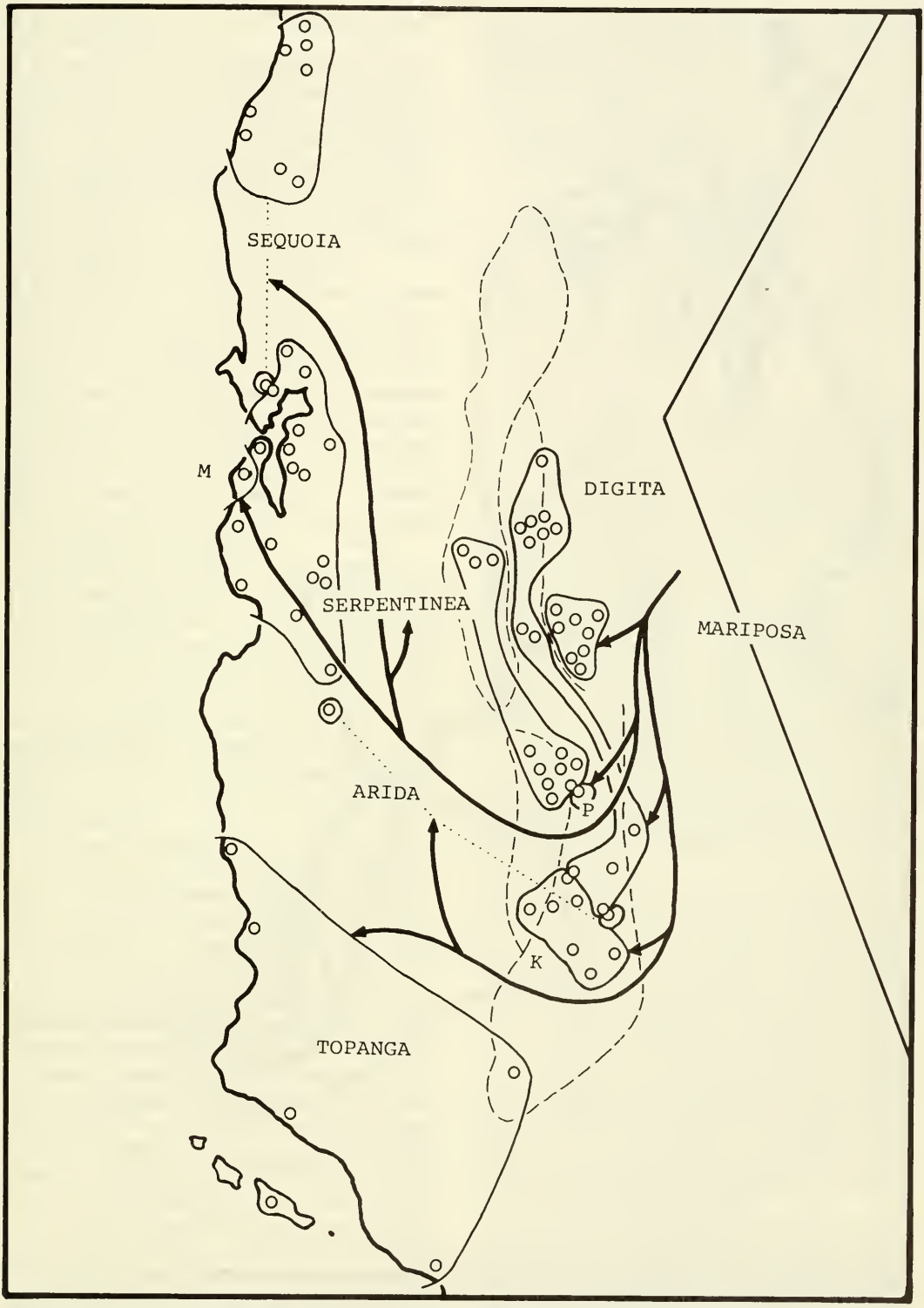

FIGURE 20. Distribution of the subgroups of *Calicina* and a cladogram of their relationships. A dotted line connects disjunct elements and a dashed line indicates the presumed boundaries of the Sierran exotic terranes (from Hendrickson 1986). Abbreviations: K = *kaweahensis*, M = *minor*, and P = *palapraeputia*.

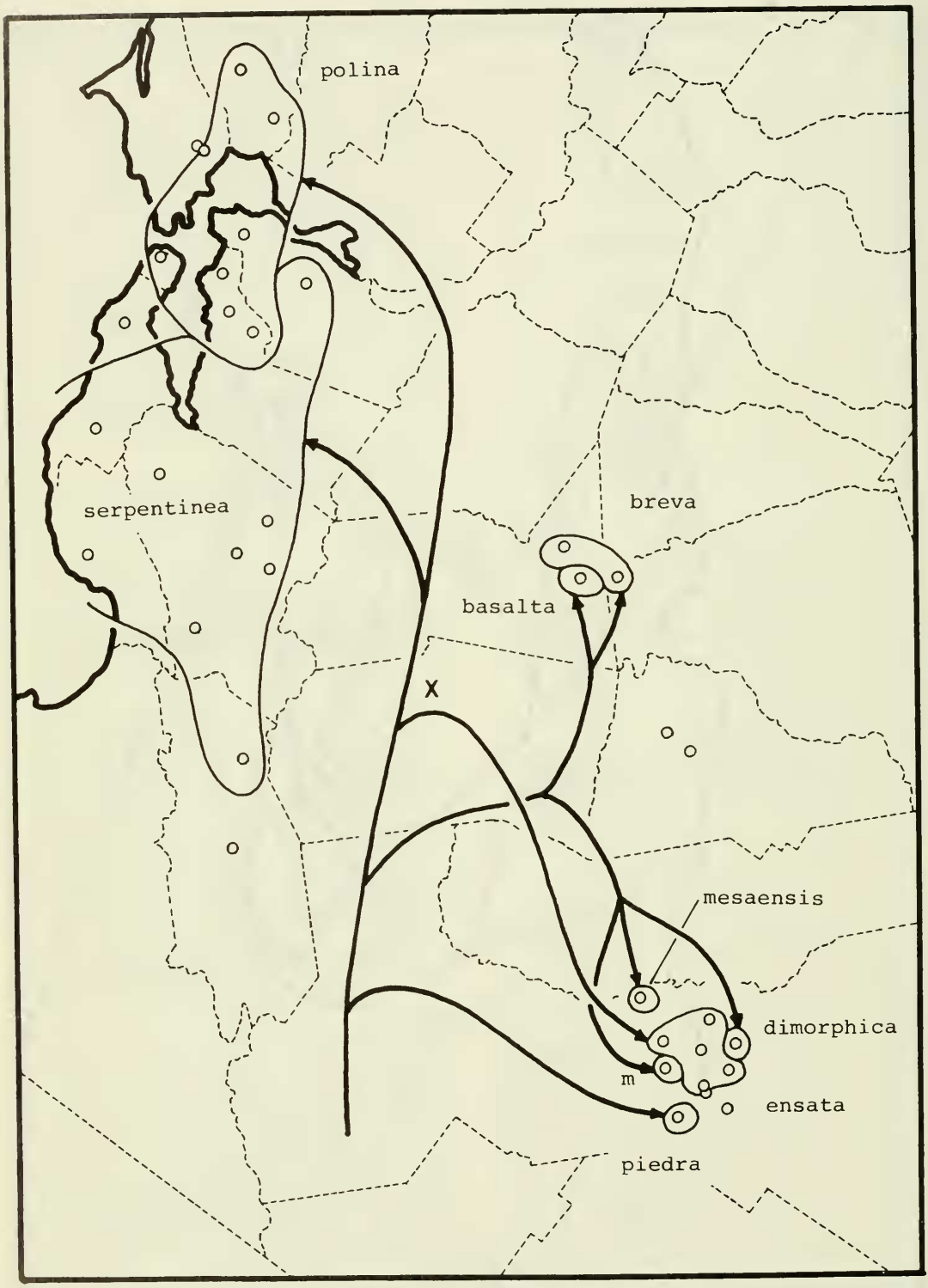

FIGURE 21. Map of central California showing the distribution of the species of the *serpentinea* subgroup with a cladogram of their relationships. The 'x' indicates the presumed time of the subgroup's disjunction by the Central Valley. Abbreviation: m = *macula*.

imity, they have never been collected in the same rock outcrops.

An area cladogram of the groups and subgroups is given in Figure 20. Two gradients are apparent. An altitudinal gradient exists between the *mariposa, digita,* and *serpentinea* groups, which occupy progressively lower elevations. A latitudinal gradient is also evident: the *digita* group occurs primarily along the southern mountains and coast, whereas the *serpentinea* group occupies the central and northern parts of the state.

The distribution pattern of the subgroups of *Calicina* is compatible with an origin through vicariance. The initial speciation events are likely to have taken place in the Sierra. The Sierran component of *Calicina* contains representatives of all four groups, including the most generalized members (*mariposa* group, *digita* subgroup, and *piedra*). The initial speciations may have resulted from two barriers (given the basal trichotomy) located between the ranges of the *mariposa, digita,* and *serpentinea* groups.

It is worth noting that these presumed barriers closely correspond to the proposed boundaries of exotic terranes given by Hendrickson (1986) and indicated in Figure 20. The coastal *Calicina* distributions also correspond closely to the maps of exotic terranes. The species *topanga* and *morroensis* each occupy separate terranes, and the coastal distribution of the *serpentinea* group (with the exception of the two westernmost *serpentinea* localities) is located within the Franciscan complex of terranes.

A few taxa exhibit disjunct distributions that, in conjunction with our knowledge of geologic history, may be used for estimating their minimum ages. The *polina* distribution surrounds the San Francisco Bay, suggesting that the species predates the formation of the bay. Similarly, *topanga* occurs on Santa Cruz Island as well as the adjacent mainland. If the currently disjunct distribution resulted from the formation of the Santa Barbara Channel, then the species must be rather old. Recent estimates for a land connection to these islands are much older (although unspecified) than the previous model of a Pleistocene land bridge (Wenner and Johnson 1980). It may be more plausible, however, that the Santa Cruz Island population represents a more recent colonization from the mainland. Rafting is a commonly evoked mechanism (for example, by Yanev (1982) for slender salamanders) and a good possibility for the forest-dwelling *topanga.*

The Central Valley is currently an obvious and impenetrable barrier for *Calicina* (owing to the absence of favorable mesic habitats) and divides the distributions of two subgroups, *arida* and *serpentinea.* The Sierran uplift, which formed the Central Valley, is thought to have begun in the early Pleistocene. A barrier could eventually have resulted from the drying effects of glacial retreats, as proposed for the populations of *Ortholasma levipes* Shear and Gruber (1983:12). Our interpretation of the *serpentinea* subgroup relationships indicates that the Central Valley could have been responsible for the disjunction of *ensata* from *serpentinea-polina* (indicated by an "x" in Fig. 21).

Another method of estimating the time of cladogenic events in *Calicina* is to use the findings for another organism from the same ancestral biota. A good example is the slender salamander, *Batrachoseps.* It appears very likely that *Batrachoseps* and *Calicina* experienced a comparable evolutionary history for three reasons: their similar habitat preferences, congruent distributions, and compatible phylogenies.

The ecological requirements of *Batrachoseps,* as described by Yanev (1980) are remarkably similar to those of *Calicina.* Both genera include species restricted to forests or oak woodlands. Both are specialized for subterranean life, appear at the surface only during favorable periods, and are able to survive in small isolates of suitable habitat. Studies on *Batrachoseps* indicate that individuals are extremely sedentary and have a very low dispersal potential, as is probably the case for *Calicina.*

The phylogeny of *Batrachoseps* consists of three main lineages. The basal branch, currently represented by two disjunct isolates, is thought to have formerly ranged along the eastern Sierra Nevada, close to that of the present distribution of the *mariposa* group. The second branch is represented by *B. attenuatus,* which has a coastal component that is almost identical to that of the *serpentinea* group and a Sierran component intersecting the distribution of *breva* and *basalta.* The third branch contains the remaining four species whose combined distribution is very similar to that of the *digita* group.

On the basis of electrophoretic and immunological studies, Yanev (1980) proposed an origin for *Batrachoseps* in the early Eocene (ca. 50 mya). However, Hendrickson (1986) criticized these values as being far too recent and suggested that

Table 3. Field Data of *Calicina*.

Taxa	N[1]	Biome	Habitat	Season[2]
mariposa gp	10	sequoia-yellow pine	snags, logs	summer
digita	9	sequoia-yellow pine, oak wood, grass	logs, gra, sla	all year
digita (cave)	1	sequoia-yellow pine	cave	spr[3]
sierra	6	digger pine-oak	lim, sch, sla	win–spr
sierra (cave)	8	digger pine-oak	caves	all year
galena	3	sequoia-yellow pine	gra, logs	summer
kaweah	12	oak wood	gra	win–spr
topanga	9	broadleaf evergreen, digger pine-oak, oak wood	logs, bas, snd, bre	win–spr[3]
kee	1	oak wood	gra	win–spr
mor	4	grass	srp	win–spr
clough	3	oak wood	cave	srp–sum[3]
arida	2	oak wood	srp	win–spr
pala	5	oak wood	gra, srp	win–spr
minor	4	grass	srp	win–spr
serp sbgp[4]	29	oak wood, grass	spr, bas, gra, snd, rhy	win–spr
serp	12	redwood-broadleaf evergreen, digger pine-oak, oak wood, grass	logs, srp, lim, snd	all year
serp (cave)	1	redwood	cave	spr[3]
diminua	3	grass	srp	win–spr
sequoia	11	redwood-Douglas fir	logs, rocks	all year

Abbreviations: N = number of collection samples; gp = group; sbgp = subgroup; kaweah = *kaweahensis*; kee = *keenea*; mor = *morroensis*; clough = *cloughensis*; pala = *palapraeputia*; serp = *serpentinea*; wood = woodland; grass = grassland; bas = basalt; bre = breccia; gra = granite; lim = limestone; rhy = rhyolite; sch = schist; sla = slate; snd = sandstone; srp = serpentine; spr = spring; sum = summer; win = winter.

[1] Roughly ¾ of all samples include biome and habitat data.

[2] Time of the year when adults are active.

[3] Probably active all year.

[4] Excluding *serpentinea*.

the isolation of *Batrachoseps* must have taken place between the late Jurassic and the early Cretaceous. This conclusion was based on the correlation between cladistic branching and geologic events, especially the history of exotic terranes.

The geologic history of the Californian terranes is still largely unresolved. Most of the terranes are believed to have distant southern origins, presumably in the vicinity of southern North America. Their northward displacement as isolated units is thought to have commenced in the mid-Mesozoic. Subsequent accretions to the North American Plate range from late Jurassic to Cretaceous for the Sierran terranes, to early Eocene for the southern coastal terranes, and to late Miocene for the western elements of the Franciscan complex. If the present distribution pattern of *Calicina* is the result of isolation on terranes, then a possible scenario is that the original breakup of the Sierran terranes isolated the ancestral populations of *Calicina*, which eventually evolved into distinct species. Following accretion to their present position, some dispersal from the terranes would be necessary to account for the present distribution, especially for the south Sierran members of the *serpentinea* group. The later arrival of the coastal terranes suggests widespread dispersal from the Sierran populations.

Natural History

Information on the natural history of *Calicina* comes from our field observations and the data associated with some 130 collection samples. This information, summarized in Table 3, is discussed below.

Habitat.—Species of *Calicina* occur in mesic habitats (in conditions of total darkness and high humidity) but are apparently absent from those areas that are periodically inundated or situated in saturated soils. Most species are found exclusively beneath medium to large-sized rocks that are in contact with the soil and undisturbed. Oth-

er species also occur beneath decomposing logs. One group of species (the *mariposa* group) is found exclusively under logs and, more commonly, beneath and among fragments of fallen bark that surround large snags. Four species have been recorded from caves. One of these (*cloughensis*) is a troglobite, the others are troglophiles with predominantly surface populations. These habitat preferences of *Calicina* are similar to those previously recorded for all Californian phalangodids (Briggs 1968) except that *Calicina,* unlike some species of *Sitalcina,* has never been collected in leaf litter.

Species of *Calicina* are associated with many rock types, the most frequent being serpentine. Of the 64 collection samples that indicate specific rock associations, 28 are from serpentine. Other frequently recorded rocks are granite (13 samples), basalt (seven), sandstone (seven), and limestone (four, excluding cave collections). The Coast Range species have been recorded primarily from serpentine and sandstone, the Sierran ones from granite and basalt.

Biome.—The species of *Calicina* are known from a variety of biomes (see also Fig. 22). Some are apparently restricted to dense forests. Members of the *mariposa* group and *galena* are known only from high elevations (1,200–2,000 m) in primary stands of giant sequoia-yellow pine association. *Calicina sequoia* has been collected only in redwood-Douglas fir association. Three additional species have been collected in dense forests. *Calicina digita* is recorded from giant sequoia-yellow pine, *topanga* and *serpentinea* from broadleaf evergreen, the latter also in association with redwood. However, these three species are also known from more open forests (digger pine-oak and oak woodland), as well as from grassland. All remaining species are known only from oak woodland and grassland biomes.

Activity.—The period of adult surface activity varies between the species. Three patterns are evident. (1) Species active during the rainy season (winter to spring). These species (14) live in grassland and oak-woodland biomes (one species from digger pine-oak). (2) Species active during the summer. Species of the *mariposa* group and *galena,* collected in the summer months, are known only from giant sequoia-yellow pine forests. (3) Species active throughout the year. The residents of dense, low-elevation forests (*sequoia* and forest populations of *serpentinea, digita,* and possibly *topanga*) have a year-long adult activity period. Likewise, the cavernicolous populations of *sierra* have been collected throughout the year. It is expected that the other cavernicolous *Calicina* also have year-round activity.

Life Cycle.—Almost all individuals of *Calicina* encountered in the field and in collections are adults. Despite repeated efforts to collect juveniles, only three subadults are known from epigean habitats (five additional juveniles are known from caves). This absence of juveniles at the surface suggests that development in *Calicina* takes place within the soil. The appearance of adults of species from drier environments coincides with the onset of the rainy season. Normally, only one or a few individuals are present on each rock or log undersurface. However, in several species we have observed aggregations of 10 or more individuals, often containing at least one mating pair.

Cohabitants.—The habitat of *Calicina* is densely populated by a rich assortment of organisms. The most commonly observed insects are campodeid diplurans and collembolans. Observations suggest that collembolans are the likely prey of *Banksula* (Briggs and Ubick 1981) and probably also of *Calicina.*

Several laniatorid opilionids live sympatrically with *Calicina. Zuma* Goodnight and Goodnight is known from dense coniferous forests at higher elevations of the Sierra Nevada. *Sitalcina* is found in forests of both coastal and Sierran regions. "*Sitalcina*" *cockerelli* Goodnight and Goodnight lives in the northern coastal coniferous forests. *Banksula* is restricted to caves of the central Sierra foothills, but has never been collected sympatrically with *Calicina.*

In the central Coast Range and Sierran foothill regions, numerous spiders are repeatedly collected with *Calicina.* Some of the more common (and distinctive) are leptonetids (*Archoleptoneta*), telemids (*Usofila*), oonopids (*Orchestina* and *Scaphiella*), amaurobioids (*Blabomma, Calymmaria, Pimus,* and *Titiotus*) and many gnaphosids. Interestingly, these taxa, with the exception of the oonopids, gnaphosids, and *Pimus,* all have local cavernicolous representatives.

Conservation.—Several *Calicina* species are known only from single localities and may be facing extinction as a result of habitat destruction. An extreme example is *arida* whose known range consists of several square meters in a small ravine, surrounded by extremely xeric or disturbed environments. Several additional species

TABLE 4. THE RELATIONSHIP BETWEEN PAEDOMORPHIC AND TROGLOBITIC CHARACTERS (TARSAL COUNT AND EYE LOSS) AND XERIC ENVIRONMENTS (OAK-GRASSLAND BIOMES) IN *CALICINA*.

Calicina species	Tarsal count	Eyesight	Biome
mariposa gp.			
mariposa sbgp.			
mariposa	3-5-5-5		
yosemitensis	3-4-4-5		
conifera	3-4-4-5	blind	
digita gp.			
digita sbgp.			
digita	3-5-5-5		xeric (most)
sierra	3-4-4-4		xeric
kaweahensis sbgp.			
kaweahensis	3-5-4-5		xeric
galena	3-5-5-5 (3-5-4-5)		
topanga sbgp.			
topanga	3-5-5-5	blind (some)	
keenea	3-4-4-5		xeric
morroensis	3-4-4-4	blind	xeric
arida sbgp.			
cloughensis	3-5-5-5	blind	
arida	3-4-4-4	blind	xeric
palapraeputia gp.			
palapraeputia sbgp.			
palapraeputia	3-4-4-5		xeric
serpentinea gp.			
minor sbgp.			
minor	3-4-4-4	blind	xeric
serpentinea sbgp.			
piedra	3-4-4-5		xeric
ensata	3-4-4-4		xeric
serpentinea	3-4-4-5	blind	xeric (most)
polina	3-4-4-4	blind	xeric
macula	3-4-4-4	blind (some)	xeric
mesaensis	3-4-4-4		xeric
dimorphica	3-4-4-5		xeric
breva	3-4-4-4	blind	xeric
basalta	3-4-4-4	blind (some)	xeric
sequoia sbgp.			
diminua	3-4-4-4	blind	xeric
sequoia	3-3-4-4 (3-4-4-4)		

are known from single localities: *basalta, cloughensis, conifera, diminua, dimorphica, keenea, macula, mesaensis, minor,* and *piedra.* Conservation programs will be necessary if these organisms and their habitats are to be protected.

ECOLOGY

Calicina exhibits considerable size-related interspecific variation. Larger species have relatively higher tarsal counts, darker pigmentation, greater number of anterior tubercles, larger tarsal spurs (of male palpi), and well developed eyes. These structures are reduced in size or absent in their smaller relatives. The possibility that one of these character clusters is synapomorphic is incompatible with our cladistic analysis, as neither group of species represents a clade. However, there appears to be a correlation between reduced size and xeric biomes (see Table 4 and Fig. 22). This section will explore the hypothesis that the character transformations result from two phenomena, paedomorphosis and troglobism, and represent adaptations to xeric conditions.

PAEDOMORPHOSIS.—The direction of the somatic character transformation can be inferred by comparison with the ancestral state. As argued in the phylogeny section, the probable outgroup for the remaining species of *Calicina* is *mariposa,* the species with the simplest (=plesiomorphic) glans morphology. The forest-dwelling *mariposa* is a large, strongly pigmented species, which has a high tarsal count (3-5-5-5), the greatest number of anterior tubercles (seven to eight pairs), a large tarsal spur, and well developed eyes. That the character states associated with large size are plesiomorphic is further supported by the condition in other Phalangodidae. With the exception of troglobitic species, virtually all remaining Nearctic phalangodids are large, strongly pigmented forest dwellers with high tarsal counts and well developed eyes. It is, thus, reasonable to suppose that the reduction in size and structure is derived.

Ontogenetic transformations were ascertained indirectly by examining the juvenile morphology. A total of eight specimens, representing five species, were examined (attempts to collect additional juveniles were not successful). All juveniles are white, lacking any of the orange pigmentation found in adults, all lack tarsal spurs, and all, with the exception of one penultimate instar (*galena*), lack anterior tubercles. Based on relative size, these specimens represent early (four individuals), middle (two), and penultimate instars (two). The only observable correlation with growth, other than size, is an increase in tarsal count. The earliest instars have tarsal counts of

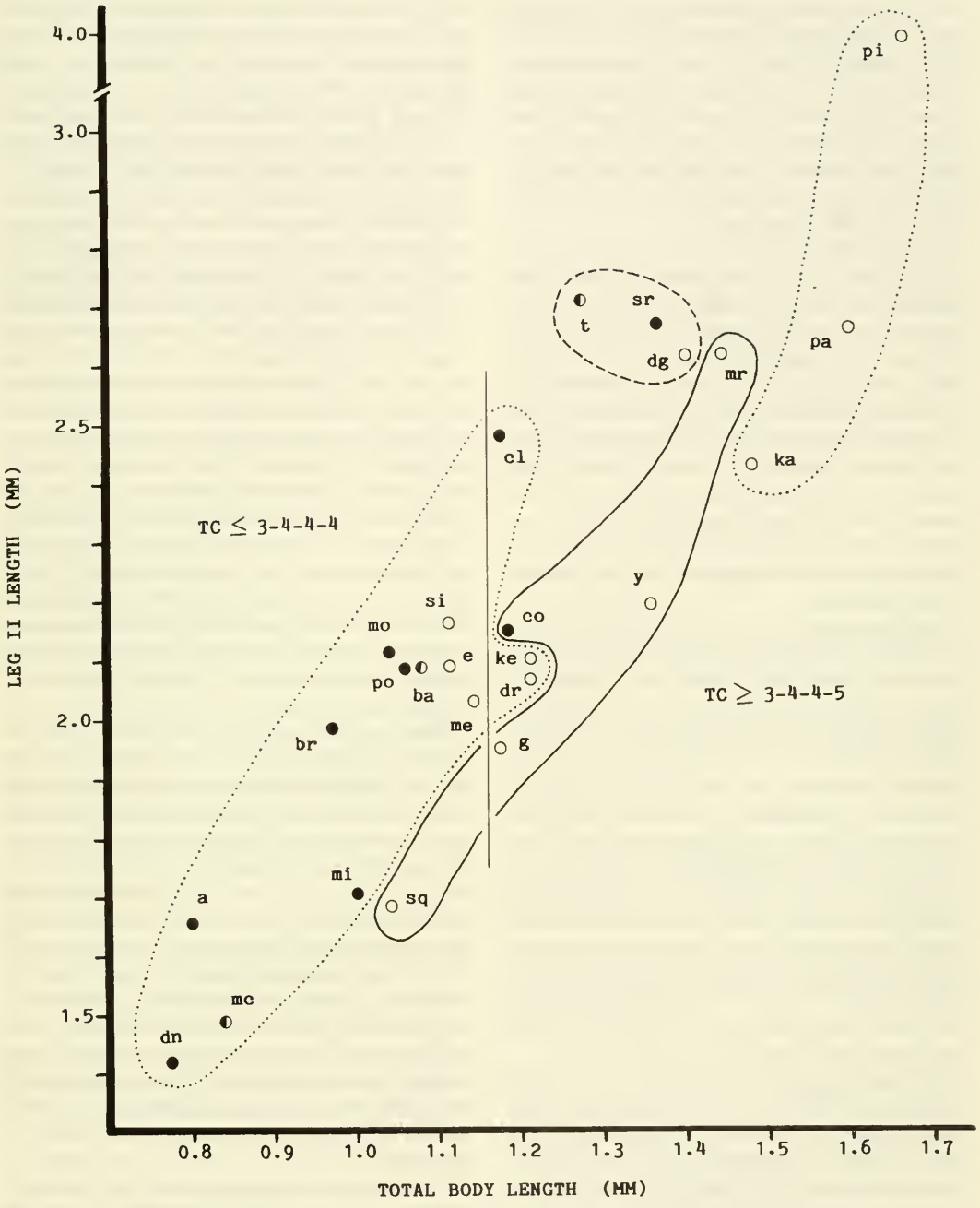

FIGURE 22. A plot showing the distribution of paedomorphic and troglobitic characters in *Calicina*. The Total Body Length and Leg II Length values are from the measurements of male holotypes (male allotypes of *digita*, *kaweahensis*, *minor*, and *serpentinea*). A circle indicates species having well developed eyes, a black dot denotes blind species, and a mixed symbol indicates the species with partial retinal loss. The vertical line separates those species with tarsal counts of 3-4-4-4 or less (paedomorphics) from those with higher counts. The forest-dwelling species are encircled by a solid line, those from oak woodland and grassland by a dotted line, and those living in both densely forested and grassland biomes by a dashed line. Abbreviations: a = *arida*, ba = *basalta*, br = *breva*, cl = *cloughensis*, co = *conifera*, dg = *digita*, dn = *diminua*, dr = *dimorphica*, e = *ensata*, g = *galena*, ka = *kaweahensis*, ke = *keenea*, mc = *macula*, me = *mesaensis*, mi = *minor*, mo = *morroensis*, mr = *mariposa*, pa = *palapraeputia*, pi = *piedra*, po = *polina*, si = *sierra*, sq = *sequoia*, sr = *serpentinea*, t = *topanga*, and y = *yosemitensis*.

1-1-2-2 (*sierra* and *sequoia*) and 1-2-2-2 (*cloughensis*); later instars (*serpentinea*) have 2-2-3-3; and the oldest (*galena*), 3-5-4-5. Eyes are present in species with eyed adults (*sierra, galena,* and *sequoia*), absent in the others (*cloughensis* and *serpentinea*). Despite the small sample size, it seems probable that these observations apply to all *Calicina,* given the generally conservative nature of juvenile characters.

Using *mariposa* as the outgroup, the character states found in the small species of *Calicina* are derived. However, a comparison with their presumed ontogeny indicates that they are plesiomorphic. The inescapable conclusion is that the small species are derived through the retention of juvenile characters; namely, that they are paedomorphic. The other possible alternative is that the juvenile states are in reality character reversals; i.e., that penultimate instars have adult somatic morphology. However, this latter possibility is clearly less parsimonious and not supported by the morphology of the two penultimates examined.

Paedomorphosis is a widespread phenomenon in *Calicina.* With the exception of three species (*mariposa, digita,* and *topanga*), all species have some degree of paedomorphic modification. However, only the 12 species having the lowest tarsal counts (3-4-4-4; 3-3-4-4 in *sequoia*) and the high correlation to other characters (see Fig. 22) are here considered to be significantly paedomorphic. Given our phylogenetic interpretations, paedomorphic species are present in all subgroups except *mariposa, kaweahensis,* and *palapraeputia,* and must have evolved independently at least nine times. Most of the paedomorphics (nine) belong to the *serpentinea* group; the remainder belong to the *digita* group, where they occupy the periphery of the group's distribution (see Fig. 19).

Paedomorphosis has been well documented in Opiliones. In her review, Rambla (1980) listed many examples of the phenomenon in Caddidae, Ischyropsalidae, Nemastomatidae, and Pentanychidae. Briggs (1986), in addition to pointing out the presence of paedomorphic *Calicina* (as *Sitalcina*) species, included Triaenonychidae among the examples.

Troglobism.—Although only one species of *Calicina* (*cloughensis*) is an obligate cavernicole, troglobitic characters are found in many species of *Calicina,* including most paedomorphics. The most obvious character is eye loss. Eight of the paedomorphic species lack retinae, along with three non-paedomorphics (excluding *cloughensis*). However, eye loss does not appear to be a paedomorphic character, as juveniles of eyed species have well developed eyes (for example, the early instars of *sierra* and *sequoia*). Additional character states of paedomorphics, such as pale coloration and small body size, could also be troglobitic adaptations. Another common troglobitic character is increased appendage length. Preliminary results (Fig. 22) suggest that the blind species of *Calicina* have slightly longer leg II lengths than comparable-sized eyed ones.

Selective Pressures.—In his exhaustive study of heterochrony, Gould (1977) differentiates two distinct phenomena included in paedomorphosis: progenesis and neoteny. Progenesis evolves (through r selection) in harsh, unstable, density-independent situations that favor rapid maturation. This is achieved by shortening the life cycle through premature maturation, and results in adults juvenilized in both size and shape. Neoteny, on the other hand, evolves (through K selection) in stable, density-dependent situations that favor maintenance. Here the selection is not for early maturation but for adaptive larval characters. Adult neotenics are, therefore, juvenilized in shape but not size.

The small size of paedomorphic *Calicina* strongly suggests progenesis. As mentioned earlier, all paedomorphic species (except *sequoia*) reside exclusively in oak woodland and grassland biomes, whereas non-paedomorphics occur predominantly in dense forests. The former biomes are much more xeric and experience severe dry seasons, which may favor both the small size and shorter life cycle of progenetics. The presence of troglobitic characters in paedomorphic *Calicina* indicates a prolonged subterranean existence, which would clearly favor a reduction in size. Also, a shorter life cycle would be an advantage in harsh environments having short growing seasons. This was postulated by Shear (1975) for another progenetic harvestman, *Caddo pepperella* Shear.

A somewhat weaker argument may be made that the paedomorphosis in *Calicina* is the result of neoteny. First, it is theoretically possible (though perhaps less parsimonious) that the reduction in size and juvenilization are independently derived; the former resulting from proportioned dwarfism, the latter from neoteny. Second, the presence of troglobitic characters in paedomorphic *Calicina* suggests cavelike selective pressures. Studies cited by Culver (1982)

indicated that certain cave salamanders become neotenic in response to a low food supply. If the subterranean habitat of paedomorphic *Calicina* is cavelike in these respects, such as constant conditions and resource scarcity, then K selection and neoteny emerge as possibilities.

Neoteny is also a possibility for the three largest species of *Calicina*: *kaweahensis, palapraeputia,* and *piedra.* In contrast to the forest-dwelling habits of other large species, these species inhabit grassland biomes. They exhibit some reduction in the tarsal count, most pronounced in the latter two (which also lack tarsal spurs on the male palpi). Large size in combination with juvenile structures suggests neoteny.

Two situations suggest a relationship between competition and paedomorphosis. First, *Calicina sequoia* is unique among the paedomorphic species. On the basis of its low tarsal count (most populations have 3-3-4-4), it is the most paedomorphic species. However, it has well developed eyes, lives in dense forests, and has a year-round activity period. Paedomorphosis here does not seem to be a response to xeric environment. Interestingly, this species is fully sympatric with another phalangodid, "*Sitalcina*" *cockerelli.* The two species not only occupy the same biomes, but share identical habitats (we have six samples containing both species). They differ most strikingly in size: *cockerelli* has a body length two to three times that of *sequoia.* It seems conceivable that paedomorphosis could have evolved in *sequoia* as a means of reducing competition for similar prey.

Second, competition may also be involved in the evolution of paedomorphosis in other *Calicina* species. The Coast Range species, from *polina* south to *morroensis,* are closely sympatric with species of *Sitalcina.* However, *Sitalcina* species are non-paedomorphic forest dwellers, whereas the coastal *Calicina* species are predominantly paedomorphics from oak woodland and grassland biomes (except for some populations of *serpentinea*). Since the original biomes for *Calicina* were most probably dense forests, it is likely that the coastal *Calicina* species also resided in forests. Perhaps *Calicina* was excluded from the more favorable environments by *Sitalcina.*

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